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FRONTISPIECE. Taxa in the revised Scale-backed Antbird (*Willisornis poecilinotus*) complex. Upper five figures are Common Scale-backed Antbird (*W. poecilinotus*); bottom three are Xingu Scale-backed Antbird (*W. vidua*). Art reproduced with permission from Plate 67, Volume 8 of *Handbook of the Birds of the World* (J. del Hoyo, A. Elliott, and D. A. Christie, 2003), Lynx Edicions, Barcelona, Spain. Paintings by Hilary Burn.
SPECIES LIMITS IN ANT'BIRDS (THAMNOPHILIDAE): THE SCALE-BACKED ANT'BIRD (WILLISORNIS POECILINOTUS) COMPLEX

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ABSTRACT.—The geographic range of the Scale-backed Antbird (Willisornis poecilinotus) encompasses Amazonia. Seven currently defined subspecies are distinguished from one another by diagnostic plumage characters except for one pair. Six pairs of subspecies are apparently parapatric and lack a known barrier to intergradation in at least a portion of their contact zone; yet confirmed hybrids are known only for one pair in one location. An analysis of >350 recordings, however, found vocal differences among them insufficient to recommend elevating subspecies to the species level with one exception. Populations in southeastern Amazonia should be considered a distinct species, Willisornis vidua (Hellmayr), Xingu Scale-backed Antbird, on the basis of their distinct loudsongs, raspy call series, and contact calls. Within the widespread Willisornis poecilinotus, Common Scale-backed Antbird, the remaining instances of parapatry without extensive intergradation provide a focus for future fieldwork to define interrelationships in contact zones and mechanisms of species recognition that may be sustaining them on independent evolutionary paths. Received 75 May 2010. Accepted 9 September 2010.

The Scale-backed Antbird (Willisornis poecilinotus) (Cabanis 1847), a widespread Amazonian complex, occupies a unique place in thamnophilid antbird evolution. Scale-backed Antbirds, as described in detail by Willis (1982), primarily forage over or near army ant swarms, but their morphology directed early taxonomists (Ridgway 1911, Cory and Hellmayr 1924) to place them in the genus Hylophylax with species that were not obligate ant-followers. Willis (1982) and other observers (e.g., Zimmer and Isler 2003) noted that Scale-backed Antbirds did not look or behave like other Hylophylax species, but it remained for a molecular study (Brumfield et al. 2007) to demonstrate that Scale-backed Antbirds evolved in the clade of army ant-following birds distant from Hylophylax species in the phylogenetic tree. The genus Dichropogon had been erected earlier (Chubb 1918) for the complex, but Agne and Pacheco (2007) found the name Dichropogon was preoccupied by a genus of asilid flies and proposed the new generic name of Willisornis in honor of Edwin O'Neill Willis, who had contributed so much to the understanding of the complex as well as other thamnophilid species.

Seven subspecies have been recognized (Peters 1951, Zimmer and Isler 2003). Almost all are readily distinguished by plumage features, primarily in females. Substantial differences in female plumage led Hellmayr (1929) to include the complex in his seminal study of geographic
forms that present more well-marked characters in females than in males, variation which he termed heterogynism. In temporal order, the seven subspecies are *W. p. poecilinotus* (Cabanis 1847), *W. p. griseiventris* (von Pelzeln 1869), *W. p. lepidonotus* (Sclater and Salvin 1880), *W. p. vidua* (Hellmayr 1905), *W. p. nigrigula* (Snethlage 1914), *W. p. duidae* (Chapman 1923), and *W. p. gutturalis* (Todd 1927). Together they populate the Amazonian lowlands (Fig. 1).

In the years since these subspecies were described, ornithological surveys in Amazonia have expanded our knowledge of their distribution and have produced a large number of vocal recordings from throughout their range. Vocal characters afford a relevant “yardstick” (sensu Mayr and Ashlock 199!) for estimating reproductive isolation and species status of sympatric and allopatric populations of suboscine passerines (Isler et al. 1998, Johnson et al. 1999, Baptista and Kroodsma 2001, Helbig et al. 2002, Remsen 2005). Recently obtained data provide an opportunity to reevaluate the taxonomic status of *Willisornis* populations based on geographic relationships among plumage-defined subspecies, and on the extent to which vocal differences among these subspecies support species status.

**METHODS**

Populations were based on geographic ranges of currently defined subspecies with two further subdivisions. Vocalizations of *lepidonotus* were divided into recordings obtained below and above 800 m elevation based on preliminary molecular analysis of J. M. Bates (pers. comm.). Vocalizations of *griseiventris* were allocated to populations east and west of the Rio Madeira because the Rio Madeira is a major barrier to gene flow in understory birds (Isler et al. 1998, Johnson et al. 1999, Baptista and Kroodsma 2001, Helbig et al. 2002, Remsen 2005). Recently obtained data provide an opportunity to reevaluate the taxonomic status of *Willisornis* populations based on geographic relationships among plumage-defined subspecies, and on the extent to which vocal differences among these subspecies support species status.

Specimens were examined at the Louisiana State University Museum of Natural Science (LSUMZ), the Museo Paraense Emilio Goeldi (MPEG), the Museo de Zoologia, Universidade de São Paulo (MZUSP), and the National Museum of Natural History, Smithsonian Institution (USNM) with additional data provided by staffs of the American Museum of Natural History (AMNH), the Carnegie Museum of Natural History (CM), the Colección Ornitológica Phelps (COP), and the Field Museum of Natural History (FMNH). Measurements of bill width, depth, and length (at nares) and tarsus, tail, and wing chord were taken with MAX-CAL electronic digital calipers, which were also used to measure the length of the white interscapular patch at the center of the back. Colors were recorded by comparison with Munsell Soil Color Charts (Kollmorgan Instruments Corp., New Windsor, NY, USA), and English color names used in verbal plumage descriptions were adapted from these charts. We developed a locality-based map (Fig. 1) of the geographic distribution of each subspecies based on sites listed in museum inventories, sites referenced in the literature, and sites of vocal recordings.

Tape and digital recordings of vocalizations were compiled from our own inventories, from unarchived contributions of other individuals, and from the Macaulay Library (ML, Cornell Laboratory of Ornithology, Ithaca, NY, USA). We examined 358 recordings (Appendix). We reviewed the documentation of recordings to identify the number and gender of individuals vocalizing. RAVEN, Version 1.3 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA) was used to make a spectrogram of every vocalization type delivered by each individual on every recording. All clearly delineated spectrograms were examined visually for characters (e.g., note shape) that might distinguish a population. Spectrograms shown in figures were selected to express typical measurements (e.g., the mean number of notes in loudsongs) and were made by exporting RAVEN files into CANVAS, Version 9.0.4 (ACD systems, Victoria, BC, Canada).

Vocal characteristics obtained for loudsongs were: (1) number of notes, (2) duration, (3) pace, (4) change of pace, (5) note shape, (6) change in note shape, (7) note length, (8) change in note length, (9) interval length, (10) change in interval length, (11) frequency (nadir, peak, and max), and (12) change in frequency. The nadir is the lowest point in the tracing of a note; peak the highest point; and maximum frequency is measured at the point of highest intensity in the note. Measurements were taken of the initial, central (in time), and terminal notes and their associated intervals. Characteristics obtained for calls were fewer as they contained fewer notes. We required pairs of measurements expressing diagnostic characters to have correlation coefficients <0.80 given the possibility that some characters might be linked by common ancestry.

Quantitative measures were obtained from spectrograms projected on a 43-cm screen using
FIG. 1. Geographic ranges of *Willisornis* populations. Symbols represent the occurrence of taxa within small geographic sectors (Isler 1997). Open square = *poecilinotus*; solid triangle = *duidae*; open circle = *lepidonotus*; solid square = *gutturalis*; open diamond = *gutturalis*; solid circle = *nigrigula*; open triangle = *vidua*. Star = two subspecies occur in sector; U surrounded by a circle = subspecies not identified. Type localities and locations are as mentioned in text.

1. "British Guiana" (exact locality unknown; type locality of *poecilinotus*).
2. Borba, Amazonas, Brazil (04° 24' S, 59° 35' W; type locality of *griseiventris*).
3. Sarayacu, Pastaza, Ecuador (01° 44' S, 77° 29' W; type locality of *lepidonotus*).
4. Igarapé Açu, Pará, Brazil (01° 07' S, 47° 37' W; type locality of *vidua*).
5. Boim, Pará, Brazil (03° 00' S, 55° 27' W; type locality of *nigrigula*).
6. Cerro Duida, Amazonas, Venezuela (03° 25' W, 65° 40' W; type locality of *duidae*).
7. São Paulo de Oliveira, Amazonas, Brazil (03° 27' S, 68° 48' W; type locality of *gutturalis*).
10. Rio Putaco, Amazonas, Venezuela (02° 50' N, 64° 25' W).
13. Sierra de Chiribiquete, Caquetá, Colombia (00° 56' N, 72° 42' W).
14. Tonantins, Amazonas, Brazil (02° 47' S, 67° 47' W).
15. Divisor; Loreto, Peru (07° 12' S, 73° 53' W).
17. Cordillera de Pantanacolla, Madre de Dios, Peru (12° 40' S, 71° 13' W).
18. Santa Cruz, Rio Eira, Amazonas, Brazil (07° 30' S, 70° 49' W).
19. Eirunepe, Amazonas, Brazil (06° 40' S, 69° 52' W).
20. Reserva Uakarai, Amazonas, Brazil (05° 26' S, 67° 17' W).
21. Carauari, Amazonas, Brazil (04° 52' S, 66° 54' W).
22. Region of the Rio Canumâ, Amazonas, Brazil (06° 46' S, 59° 07' W).
23. Altas Florestas, left bank Rio Teles Pires (09° 50' S, 55° 54' W).
25. Mato Grosso, Brazil (26° 30' N, 52° 00' W).
26. Bosque de Guapié, Vichada, Colombia (08° 18' N, 67° 57' W).
27. Vicinal Aporui, 12 km north of Caracarai, Roraima, Brazil (01° 59' N, 61° 45' W).
species to the distribution of DBMs of the
compared the DBM between the two compared
sample population pairs, with replacement, and
same sample sizes. The method generated 10,000
analyzed and two groups of generated data of the
statistical significance. We compared Difference
non-parametric bootstrap simulation to examine
were not normally distributed. Thus, we used a
distribution for

Between Means (DBM) of the two taxa being
population with the larger set of measurements (a)
and the
(b) with the smaller set of measurements
and standard deviations (SD) of the population
sizes was estimated by requiring the means ($x$)
that ranges would not overlap, and the likelihood
variables could not overlap, and the potential
signal recognition (Isler et
al. 1998, 1999). Ranges of samples of continuous
ranges would not overlap with larger sample
sizes was estimated by requiring the means ($x$)
and standard deviations (SD) of the population
with the smaller set of measurements ($a$) and the
population with the larger set of measurements ($b$)
to meet the test:

$$
\bar{x}_a + t_aSD_a \leq x_b - t_bSD_b
$$

where $t_i$ = the $t$-score at the 97.5 percentile of the $t$ distribution for $n - 1$ degrees of freedom.

A similar test could not be used for ratios which were not normally distributed. Thus, we used a non-parametric bootstrap simulation to examine statistical significance. We compared Difference Between Means (DBM) of the two taxa being analyzed and two groups of generated data of the same sample sizes. The method generated 10,000 sample population pairs, with replacement, and compared the DBM between the two compared species to the distribution of DBMs of the

simulated populations. The result was distributed normally, and significance was assigned according to the rules of this distribution.

We recommend species status under the Biological Species Concept (BSC) for populations that differed diagnostically in both vocalizations and morphology. We accepted current subspecies definitions as reflecting diagnostic morphological differences described in the literature (Cory and Hellmayr 1924, Zimmer 1934, Ridgely and Tudor 1994, Zimmer and Isler 2003) after finding them to be consistent in large series of specimens examined at major museums. Vocal differences were considered diagnostic if the analysis revealed three or more diagnostic characters following the “yardstick” developed by Isler et al. (1998). For brevity, we use subspecies names to reference populations.

RESULTS

Subspecies differed from their geographic neighbors by at least one diagnostic plumage character in every instance (100% diagnosable) with the exception of duidae and lepidotus, and apparent hybrids between poecilinotus and duidae. We examine the biogeography of parapatric populations after reporting the results of vocal analyses.

Vocalizations

Vocal repertoires of Willisornis populations include five principal vocal types: (1) loudsongs, (2) contact calls, (3) chirrs, (4) raspy series, and (5) other calls. Softsongs were recorded too infrequently to be useful in the analysis.

Loudsongs.—All subspecies deliver a series of long, upslurred notes separated by shorter intervals, the series generally rising in pitch (Fig. 2). Individual variation of loudsong characteristics within populations was high. For example, of 37 loudsongs analyzed for poecilinotus, nine contained 3–5 notes, 11 contained 6–8 notes, 13 contained 9–11 notes, and four contained 12–15 notes. The unusually large variability could not be related to gender or age in our samples. No diagnosable differences in loudsongs were found between populations as a consequence of the large within-population variability with one exception. Notes of nigrigula and vidua were frequency-modulated in an even pattern, whereas such modulation was erratic or lacking in loudsong notes of the other subspecies (Fig. 2). Differences in note shape allowed perfect allocation of loudsong recordings to the two groups, and
differences in quality were apparent in the field and laboratory to the human ear.

Differences in loudsong characteristics among other populations did not meet our criteria as diagnostic, but when values were plotted geographically, distributional patterns emerged that may prove relevant to future species-level analysis. For example, frequency measures of the first note of *poecilinotus* loudsongs (37 individuals) were higher pitched than those of *duidae* (18 individuals), and ranges barely overlapped. When these frequency characters were mapped geographically, the extreme examples of each population occurred at considerable geographic distance from the contact zone, and loudsongs recorded closest to the contact zone (although only 2 individuals of each taxon) differed substantially.

Similar differences were found between *duidae* and *lepidonotus* loudsongs with *duidae* notes delivered at lower frequencies and a slower pace. For example, the mean of the lowest frequency of the central note of *duidae* was 1,948 Hz (range = 1,332–2,177, SD = 242, n = 18), whereas that of *lepidonotus* was 2,302 Hz (range = 2,177–2,678, SD = 128, n = 24), but the difference did not meet our significance test. Plotting frequency and pace geographically did not suggest a tendency for *duidae* loudsongs either to diverge or converge clinally with *lepidonotus*, although recordings are needed from the region where these populations are likely to come into contact. No significant

differences were found with regard to elevational differences within *lepidonotus*, even though a small sample of higher elevation loudsongs tended to be higher pitched and faster.

Initial notes of *griseiventris* loudsongs in general were lower-pitched than the equivalent *lepidonotus* notes, but loudsongs of the westernmost population of *griseiventris*, nearest the range of *lepidonotus*, were highest in frequency and closest to notes of *lepidonotus*, suggesting clinality. We identified no differences in *griseiventris* loudsongs east and west of the Rio Madeira.

**Contact Call.**—These calls consist of abrupt notes given when flying between perches as well as when perched. They differed diagnostically between what we termed a *twitter*, which is found only in the repertoires of *nigrigula/vidua*, and a *psit*, which is delivered only by the remaining populations (Fig. 3). The *twitter* is a short (2–16, typically 3–5), high-pitched series of clear, almost tinkling, musical notes (Fig. 3A) Each note bends slightly downward in frequency; the series descends slightly in frequency; and intervals between notes with rare exceptions lengthen slightly (typically from 60 to 75 millisec, extremes 34 and 112 millisec). Notes, especially the initial note, often start with a small hook (Fig. 3A). In contrast, the *psit* note was shaped like an inverted U or V, usually sounding lower-pitched and harsher to the human ear than the *twitter*. The *psit* was typically given singly (Fig. 3B and C), but occasionally in short series that usually decreased in frequency, sometimes dramatically so (Fig. 3D and E).

The duration of the *psit* call varied among populations. The mean length in northern lowland populations (*poecilinotus, dutiae*, and lowland *lepidonotus*) was 0.093 sec (range = 0.071–0.118, SD = 0.0120, n = 20; Fig. 3B), whereas the mean for highland and southern populations (highland *lepidonotus and griseiventris*) was 0.054 sec (range = 0.047–0.063, SD = 0.0051, n = 20; Fig. 3C). The difference was diagnosable under our criteria. However, when four examples for *gutturalis* were added to the highland and southern populations, the mean and variance were slightly larger 0.055 sec (range = 0.047–0.069, SD = 0.0066, n = 24), narrowly failing our statistical test.

**Chirrs.**—This call consisted of a short series (duration: $\bar{x} = 0.596 \pm 0.189$ sec, range = 0.248–1.020 sec, n = 52) of abrupt (5–9 millisec) notes, vertical on a spectrogram, repeated rapidly (~5
notes in 0.1 sec), and typically descending in pitch (e.g., apex of notes ~ 5 mHz descending to ~4 mHz) (Fig. 4A). Chirrs have been recorded for all populations. No diagnostic differences in chirrs were found among *Willisoris* populations, although the duration of chirrs of *nigrigula* and *vidua* overlapped only slightly. Average chirr duration in *nigrigula* recordings was 0.728 ± 0.209 sec, range = 0.420-1.020, n = 10), whereas that of *vidua* was 0.399 ± 0.053 sec, range = 0.322-0.444, n = 6). Difference in means met student's t-test at 99%. At times chirrs were combined with contact calls.

**Raspy Series.**—Notes in raspy series were typically repeated 2–4 times but were sometimes given individually or in longer series. Typical *poecilinotus* calls had “U” shaped notes (Fig. 4B); the series descending slightly in pitch, sounding like “cheery, cheery, churry, churry.” The call of *griseiventris* typically had the initial part of the note truncated, making it look like a “J” in a spectrogram, and the base of the notes typically rose slightly in frequency (Fig. 4C). Few calls were available for *duidae, lepidonotus, and gutturalis*, but they suggested intermediacy between *poecilinotus* and *griseiventris* and, consequently, differences among these five subspecies were not considered diagnostic. We suspect that analysis of larger samples may detect diagnostic differences in raspy series among these populations. Note shapes in raspy series of *vidua* and *nigrigula*, in contrast, differed consistently from those of other

populations. Notes delivered by *nigrigula* and *vidua* (Fig. 4D) lacked the down-pitched beginning of the note and had a flat or sometimes ascending, vibrant base of wider frequency range than notes of the other populations.

**Other Calls.**—Calls other than contact calls, chirrs, and raspy series were relatively rarely recorded and, in most instances, the recordist did not clearly attribute the call to a *Willisornis* population. Four differently shaped calls have been recorded, including down-slurred, inverted U shaped, and upslurred notes. The most common type was down-slurred, ~0.2–0.4 sec in duration, and descending generally in the range of 4.0 to 1.5 mHz (Fig. 5A). Calls of this type were found in recordings of *griseiventris, nigrigula, vidua,* and *lepidonotus* above 800 m. A longer (0.45–0.6 sec), higher pitched, down-slurred (6 to 4 mHz) ‘‘pseer’’ (Fig. 5B) has been recorded twice for *poecilinotus*. Short (~0.25 sec), inverted U shaped notes sounding like an abrupt ‘‘wheat’’ were recorded for *poecilinotus* in the 2.6–3.4 mHz frequency range (Fig. 5C) and in the 1.9–2.3 mHz frequency range (Fig. 5D) for *gutturalis* in which the notes were doubled, for *lepidonotus* below 800 m in a short series (Fig. 5E), and for an uncertain population near the contact zone between *gutturalis* and *griseiventris*. An abrupt upscale note given in series was recorded for *griseiventris* (Fig. 5F) and for *lepidonotus* below 800 m. The meager data suggest differences in other calls between northern and southern populations may be identified with a larger number of recordings.

Little is known of the functions of vocalizations in the *Willisornis* complex. K. J. Zimmer observed and tape-recorded a display by a male *nigrigula* in the presence of a female-plumaged individual in August 1991 near the Rio Cristalino, Mato Grosso, Brazil. Perched on a slender diagonal branch ~0.7 m above the ground, the male drooped his wings, stretched his neck up vertically, and extended his head up and down rapidly on a vertical axis, calling continuously all the while. The calls included raspy series and chirrs, and other calls, and are the only indication we had of the behavioral role of these vocalizations.

**Biogeography of Parapatric Populations**

Biogeographic analysis indicated numerous instances of apparent parapary between morpho-
logically distinct neighbors. Populations separated by the Amazon River (poecilinotus with griseiventris, nigrigula, and vitula; duidae with gutturalis and griseiventris; and lepidonotus with gutturalis) were considered to be allopatric rather than parapatric as gene flow between them is highly unlikely. We provide brief summaries of morphological distinctions and consider biogeographic relationships between neighboring pairs of parapatric subspecies starting with poecilinotus and duidae in the north and proceeding counterclockwise around the Amazon Basin (localities provided in Fig. 1).

**Contact Between W. p. poecilinotus and W. p. duidae.**—Females are distinguished by gray underparts in poecilinotus (brown in duidae) and buffy “scales” on the lower back of poecilinotus (white in duidae). Males differ only by a smaller interscapular patch in poecilinotus. Geographic ranges of poecilinotus and duidae are only partially delimited by rivers. The Rio Orinoco may separate the subspecies at the northernmost end of their contact zone. The most proximate specimen locations are from Caño Usate (COP, poecilinotus) and Campamento Manaka (COP, duidae), Amazonas, Venezuela, ~90 km apart. The Rio Orinoco lies between these locations as well as between Caño Usate and Colombian specimens from Vichada (Instituto Humboldt). Ranges of poecilinotus and duidae at the southern end of their contact zone in Amazonas, Brazil, extend to the left and right banks of the lower Rio Negro, respectively. Extensive fieldwork did not find either taxon on the many islands (Anavilhanas Archipelago) in this broad river (Cintra et al. 2007), although duidae occupies some islands in the upper Rio Negro near São Gabriel da Cachoeira. No barrier appears to prevent antbirds from coming into contact in the region between the upper Orinoco and the right bank of the Rio Branco; poecilinotus alone appears to occupy the area below the Rio Branco south to the Amazon. Apparent hybrids have been collected in the Valle de los Monos on the southern slope of Mt. Duida, Amazonas, Venezuela, where poecilinotus has been collected on the southeastern slope and duidae on the western slope. As described by Zimmer (1934) and corroborated by reexamination of the pertinent specimens by MLI, one (AMNH 273015) of five females collected closely resembles duidae, one (AMNH 273017) is indistinguishable from poecilinotus, and the remaining three (AMNH 273015, 273018, 273686) have a mixture of ventral and back scale coloration of the two populations. The most proximate locations to the southeast of Mt. Duida in Venezuela are Rio Putaco (COP, poecilinotus) and Ocamo (AMNH, duidae), ~100 km distant. Further southeast in Brazil, an even greater distance, ~280 km, separates specimens from the Rio Dimiti in Amazonas and the vicinity of Caracaraí, Roraima, although the intervening region is poorly studied ornithologically. No hybrids other than those from Mt. Duida are known.

**Contact Between W. p. duidae and W. p. lepidonotus.**—Chapman (1923) described the duidae male as paler gray below, the female as more reddish and brighter throughout compared to lepidonotus. In addition, the interscapular patch was found to be smaller in duidae (Zimmer 1934). Chapman’s original description and Zimmer’s (1934) analysis were based on specimens from near the extremes of their ranges: Venezuela and northwestern Brazil for duidae and Peru and Ecuador for lepidonotus. Later Colombian specimens from along the base of the Andes in Meta were identified as duidae and those from western Caquetá and Putumayo as lepidonotus (Meyer de Schauensee 1964). Most recently, the population in the Sierra de Chiribiquete, Caquetá, Colombia, was identified as duidae (Stiles et al. 1995) which, along with the population in Tonantins, Amazonas, Brazil (CM), closes the gap between their ranges. However, a sufficient series of specimens from the intermediate region in Colombia has not yet been procured to examine possible clinality in morphological characters.

**Contact Between W. p. lepidonotus and W. p. griseiventris.**—Females are distinguished by brown underparts in lepidonotus (gray in griseiventris) and white “scales” on the lower back of lepidonotus (absent in griseiventris). Males do not differ diagnostically. The Rio Ucayali separates the ranges of lepidonotus and griseiventris in central Peru. However, further south towards the headwaters of the Rio Ucayali, no river appears to perform this function. The closest confirmed locations are Kiteni; Cuzco (LSUMZ) for lepidonotus and the east slope of Cordillera de Pantiacolla, Madre de Dios (FMNH), for griseiventris. These locations are ~190 km apart and are separated by mountainous terrain with elevations >2,000 m. There are more proximate locations to the north in intervening terrain of lower elevation cited in the literature with unidentified subspecies.
Contact Between W. p. gutturalis and W. p. griseiventris.—Females are distinguished by brown underparts in gutturalis (gray in griseiventris) and white "scales" on the lower back of gutturalis (absent in griseiventris). Females of gutturalis also typically have crown redder than back (concolor in other populations). Males of gutturalis have black throat patches (absent in griseiventris). The geographic range of gutturalis is the smallest of any subspecies, restricted in Peru and Brazil to the region immediately south of the Amazon and east of the lower Rio Ucayali (Fig. 1). The extent of its range to the east and south is unclear. The likelihood that the Rio Juruá provides a barrier in a section of their contact zone is supported by specimens of female gutturalis from Eirunepé (formerly João Pessôa) on the left bank of the Juruá and by male griseiventris from Santa Cruz on the Rio Eiru, a right bank tributary (Pinto 1942, 1978; specimens examined at MZUSP). However, sight records from both banks of the Rio Juruá at the Reserva Uacarai were identified as griseiventris (Andrew Whittaker, pers. comm.). To the southwest, in the Juruá–Ucayali interfluviuum, griseiventris has been found at Divisor, Loreto, Peru, and at two other locations west of the Sierra del Divisor (Vriesendorp et al. 2006:195). Consequently, known ranges of gutturalis and griseiventris are separated by ~280 km of probably suitable habitat in this region with no river barriers.

Contact Between W. p. griseiventris and W. p. nigrigula.—The extension of the gray of the underparts to the sides of the head (ear coverts and lores) distinguishes female nigrigula from griseiventris. Males of nigrigula have a black throat, while throats of male griseiventris are plain gray. The Rio Canumã and, continuing further upstream, the Rio Sucunduri, separates their ranges (regions of locations 22 and 24; Fig. 1). However, the range of griseiventris passes the headwaters of the Rio Sucunduri to reach the Rio Tapajós above Jacareacanga, where it overlaps nigrigula and may hybridize with it locally (BMW observations and recordings of both taxa). Beyond this point, to the south, only griseiventris has been found on the left (west) bank of the Rio Tapajós and its major tributary, the Rio Teles Pires, whereas nigrigula occurs on the right (east) bank of these rivers.

Contact Between W. p. nigrigula and W. p. vidua.—Males of nigrigula have discreet black throat patches which are absent in vidua, the throat of which tends to be more whitish than its gray underparts. Females of vidua differ from nigrigula by having flanks suffused reddish-yellow-brown (slightly tinged in nigrigula) and wing edgings grayish-brown (reddish-yellow-brown in nigrigula). Interscapular patches are larger in nigrigula (15–20 mm) than in vidua (0–10 mm). The known geographic ranges of nigrigula and vidua with one exception are separated by a wide geographic gap west of the Rio Xingu (Fig. 1), although much of the region between the known ranges of these populations is unexplored ornithologically. The only known convergence of nigrigula and vidua is based on sight records by BMW in September 1994 of males within ~1 km of each other at Riozinho, Area Indigena Kayapo, Para; it cannot be considered definitive, but does serve to suggest the possibility of parapatry of these forms in this poorly studied region.

DISCUSSION

Diagnostic differences in loudsongs, raspy series, and contact calls were documented between two groups of taxa that were also distinct in plumage: nigrigula and vidua of southeast Amazonia, and the remaining populations. However, compared to other widespread Amazonian thamnophilid complexes studied by the authors (e.g., Isler et al. 2007a, b), relatively few vocal differences meeting our guidelines for species status were found among other populations in the Willisornis complex. Consequently, we recommend the complex be considered to consist of two species and seven subspecies:

**Willisornis poecilinotus** (Cabanis)—Common Scale-backed Antbird

- *W. p. poecilinotus* (Cabanis)
- *W. p. duidae* (Chapman)
- *W. p. lepidonotus* (Sclater and Salvin)
- *W. p. griseiventris* (von Pelzeln)
- *W. p. gutturalis* (Todd)

**Willisornis vidua** (Hellmayr)—Xingu Scale-backed Antbird

- *W. v. nigrigula* (Snethlage)
- *W. v. vidua* (Hellmayr)

The proposed English name of *W. vidua* is taken from the major river that flows through the center of its geographic range.

Within each of these two groups, differences in
plumage characters, such as the presence/absence of a black throat patch, served to distinguish almost all subspecies at the 100% level. The single exception was duidae and lepidonotus, whose differences in coloration (redder female, paler male in duidae) may or may not prove to be clinal when additional specimens are obtained in Colombia. The clear differences in plumage characters led us to concentrate our analysis on the biogeographic relationships between members of pairs of parapatric populations. Considering duidae and lepidonotus as a single taxon (lepidonotus has priority), locality data indicated that geographic ranges of five pairs of taxa (poecilinotus/lepidonotus, lepidonotus/griseiventris, guturalis/griseiventris, griseiventris/nigrigula, and nigrigula/vidua) were not separated, or only partially separated, by wide river barriers. Large geographic gaps in our knowledge of the taxa occupying these potential contact zones currently prevents us from ascertaining whether: (1) some or all of these plumage-defined populations are evolving independently and deserve species status under the BSC; (2) there is widespread intergradation between neighbors; or (3) secondary contact of populations is only incipient, and the evolutionary dynamic in regions of overlap is yet to unfold. Consequently, we reserve judgment on the possible species status of the taxa listed as subspecies. Field work in potential contact zones is needed not only to obtain morphological data and material for genetic analysis, but also to record vocalizations. Differences in vocal characters between these populations did not meet our conservative requirements to be diagnosable, but recordings from contact zones may provide a different perspective. Geographically fine-grained recording of loudsongs can provide a test of whether vocalizations converge or diverge in contact zones, and it is possible that calls rarely recorded for the complex may differ diagnosably.

Collections of specimens and vocal recordings are needed from the Andean foothills (>800 m) population of lepidonotus given the suggestion in vocalizations and preliminary molecular studies that it may be distinct from lowland populations. The two available examples of the contact call of lepidonotus >800 m were short in duration and therefore similar to that of griseiventris.

Genetic analysis now underway at FMNH (J. M. Bates, pers. comm.) should provide relevant insights into the phylogenetic relationships of these taxa including whether members of parapatric pairs are closest relatives. Early results showed 6.8% divergence in two mitochondrial genes between nigrigula and griseiventris across the Rio Teles Pires near the confluence of the Rio Cristalino; 0.6% divergence of griseiventris between left bank Teles Pires and right bank Rio Jiparaná; 0.5% divergence between nigrigula on right bank Teles Pires and two sites (Serra dos Carajás and 52 km S Altamira) of vidua (Bates et al. 2004). In addition, a study of speciation in the region of the upper Rio Negro in northwestern Brazil found 10.8% genetic divergence between poecilinotus and duidae (Naka 2010). Differences in duration of contact call notes of Willisornis populations north and south of the Amazon suggest an early divergence that should be relevant to evolutionary studies as well as systematics.

Current knowledge provides only the “tip of the iceberg,” and valuable insights relevant to systematics, conservation, and broader studies of evolution await further investigation of the Willisornis complex.

ACKNOWLEDGMENTS

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APPENDIX

Recordings Examined.—The following list identifies recordings used in the study by taxon, country, state or department, recording location, and recordist. Numbers following the recordist name identify the number of cuts per recordist per location. Acronyms for recording archives: BSA = Banco de Sonidos Animales, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá. FSM = Florida State Museum Sound Archive. ML = Macaulay Library, Cornell Laboratory of Ornithology, Ithaca; ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by Morton and Phyllis Isler. Many of these unarchived recordings either are in the process of being archived or will eventually be archived by the recordists. Nomenclature reflects recommended taxonomic position.

*Willisornis p. poecilinotus*: (53 recordings; 24 locations). Brazil: Amapá: Porto Grande (Zimmer 3 ISL); Amazonas: Rio Apuatu (Cohn-Haft 1 ISL), 60–90 km N Manaus (Bierregaard 1 ML, Stouffer 1 ML, Whitney 1 ISL, Whittaker 1 ISL), Reserva Ducke (Whitney 1 ISL), Guyana: Acarai Mountains (Robbins 1 ML), Baramita (Brumfield 1 ISL), Ivokrakama Forest Reserve (Whitney 5 ISL), Kaiteur Fall (Milenisky 1 ISL), Kako River (Robbins 2 ML), Kopianga (O'Shea 1 ML), Kuyuwini River (Finch 2 ML), Marshall Falls (Finch 1 ML), Nappi Village (Parker 1 ML), Sipu River (Milenisky 1 ISL), Waruma River (O'Shea 1 ML). Suriname: Brownsberg Nature Reserve (Davis 2 ML, Whitney 2 ISL), Kraka-Zenderij Road (Whitney 1 ISL), Raleigh Vallen (Whitney 1 ISL), Voltzberg (Davis 1 ML, M. Isler 1 ML, Whitney 1 ISL). Guyana: Amazonas: Jungla-ven Camp (Zimmer 1 ISL); Bolívar: El Palmar (Parker 2 ML, Schwartz 3 ML), La Escalera (Behrstock 1 ISL, M. Isler 1 ML, Macaulay 1 ML, Schwartz 1 ML, Whitney 1 ISL, Zimmer 2 ISL), 20–30 km SE Maripa (Stejskal 1 ISL, Whitney 2 ISL), Sierra de Lema (Behrstock 1 ISL, Zimmer 1 ISL).


*Willisornis p. lepidonotus* below 800 m: (37 recordings; 18 locations). Ecuador: Morona-San-tiago: Miazal (Whitney 1 ISL), Santiago (Robbins 1 ISL); Napo: La Selva Lodge (Behrstock 1 ISL, Coopmans 2 ML, Donahue 1 ML, Wolf 2 ISL), km 37 Maxus Road (Krabbe 3 ISL), Tiputini Biodiversity Station (Behrstock 1 ISL, Zimmer 2 ISL); Pastaza: Kapawi Lodge (Whitney 1 ISL, Wolf 1 ISL); Sucumbios: Cuyubeno (Whitney 1 ML). Peru: Loreto: Colonia Angamos (Lane 1 ISL), 79 km WNW Contamana (Lane 3 ISL), El Dorado (Whitney 3 ISL), El Tigre (J. Alvarez 3 ISL), Explorama Lodge (Whitney 1 ISL), Intuto (Whitney 1 ISL), Quebrada Orán (Whitney 2 ISL), Quebrada Sucusari (P. Isler 1 ML), Sachacocha (J. Alvarez 1 ISL), Yanamono (Budney 2 ML, Whitney 1 ISL); San Martín: Tarapoto- Yurimaguas Road (Lane 1 ISL).

*Willisornis p. lepidonotus* above 800 m: (16 recordings; 8 locations). Ecuador: Napo: 15 to 80 km W of Loreto by road (J. Rowlett 1 ISL, R. Rowlett 1 ISL, Whitney 2 ISL, 1 ML, Wolf 1 ISL), Volcán Sumaco (R. Rowlett 1 ISL); Zamora-Chinchipe: Parque Nacional Podocarpus (Wolf 1 ISL). Peru: Cajamarca: Cordillera del Cóndor, (Schulenberg 1 ISL), Puesta Vigilancia (Schulenberg 1 ML); Loreto: 77 km WNW Contamana (Lane 3 ISL), ~90 km SE Juanjui (Lane 2 ISL); San Martín: Jirijio, 15 km NE (Schulenberg 1 ML).

*Willisornis p. gutturalis*: (12 recordings; 3 locations). Brazil: Amazonas: Benjamin Constant (Whitney 4 ISL), R. N. Palmarí (Whitney 5 ISL,
Zimmer 1 ISL. Peru: Loreto: Tahuayo Lodge (Hornbuckle 2 ISL).

*Willisornis p. griseiventris*: W of Madeira: (40 recordings; 23 locations). Bolivia: La Paz: Campamento Nuano (Tello 1 ISL), Chalalán (Whitney 1 ISL), Cadena Pilón (Parker 1 ISL), Puerto Linares (Wiedenfeld 1 ML), Serranía Tequeje (Hennessey 1 ML); Pando: Rio Abuña, (Parker 1 ISL), Camino Mucden (Parker 3 ML), 12–20 km SW Cobija (Parker 1 ISL), San Juan de Nuevo Mundo (Parker 1 ISL). Brazil: Acre: Boca de Tejo (Whittaker 2 ISL); Amazonas: Amazon Lodge (Zimmer 2 ISL), Humaitá (Whitney 3 ISL), Lábrea (Whitney 1 ISL, Zimmer 1 ISL), Igarapé Santa Maria (Whitney 1 ISL), Tefé (Pacheco 1 ISL), Fazenda Toshiba (Marantz 1 ML), Tupana Lodge (Zimmer 4 ISL), Uará (Whittaker 1 ISL). Peru: Madre de Dios: Cuzco Amazonica Lodge (Marantz 1 ML), Explorer’s Inn (Donahue 1 ML, M. Isler 1 ML, Kibler 3 ML, Parker 2 ML), Cordillera del Pantacolla (Fitzpatrick 2 ML); Puno: Campamento Topo Tres (Schulenberg 1 ISL); Ucayali: Cerro Tahuayo (Meyer 1 ISL).

*Willisornis p. griseiventris*: E of Madeira: (74 recordings; 25 locations). Bolivia: Santa Cruz: Flor de Oro (Whitney 1 ISL), Los Fierrros (Whitney 2 ISL), Perseverancia (Fisher 1 ISL, Parker 1 ISL, 1 ML). Brazil: Amazonas: Rio Atíninga (Whitney 1 ISL), Rio Bararati (Whitney 5 ISL), Barra de São Manuel (Whitney 4 ISL), Borba (Whitney 1 ISL, Whittaker 1 ISL), Nova Olinda (Rio Arupuaná (Whitney 1 ISL), Rio Ipixuna (Whitney 1 ISL), Puxurizal (Marantz 1 ML, Whitney 1 ISL), mouth of Rio Palomitas (Whitney 4 ISL), Pousada Jurumê (Whitney 2 ISL), Pousada Rio Roosevelt (Whittaker 2 ISL), Zimmer 1 ISL), Prainha Nova (Whitney 1 ISL), L bank Rio Sucunduri near BR 230 (Whitney 5 ISL); Mato Grosso: Alta Floresta (M. Isler 2 ISL, P. Isler 1 ISL, Parker 2 ISL, Whitney 3 ISL, Zimmer 5 ISL), R bank Rio Juruená opposite mouth Rio Bararati (Whitney 1 ISL), mouth of Rio São Benedito (Whittaker 1 ISL), mouth of Rio São Tome (Whitney 2 ISL); Rondônia: Rio Caracol (Whitney 1 ISL), R bank Rio Jiparaná opposite Palmeiras (Whitney 3 ISL), Serra dos Pácaás Novos (Whittaker 3 ISL), Palmeiras (Whitney 4 ISL), Porto Velho (Whitney 6 ISL), Fazenda Rancho Grande (Zimmer 3 ISL).

*Willisornis vidua nigrigula*: (47 recordings; 15 locations). Brazil: Amazonas: Igarapé Pedral (Whitney 4 ISL), Igarapé do Seringal (Whitney 2 ISL), 52 km W Jacareacanga (Whitney 1 ISL), R bank Rio Sucunduri near BR 230 (Whitney 3 ISL); Mato Grosso: Rio Cristalino (Michael 1 ML, Whitney 2 ISL, Zimmer 8 ISL); Pará: Parque Nacional de Amazonia (Whittaker 5 ISL), Aveiro (Whitney 3 ISL), Boim (Whitney 1 ISL), Cachimbo (Whittaker 1 ISL), Capelinha Trail (Parker 1 ML), km 209 S of Itaituba (Whitney 3 ISL), Jacareacanga (Whitney 3 ISL), Mirítuba (Whitney 3 ISL, Willis 3 FSM), Porto do Meio (Whitney 1 ISL), Riosinho (Whitney 1 ISL), Rurópolis (P. Isler 1 ML).

*Willisornis v. vidua*: (39 recordings; 6 locations). Brazil: Pará: Serra dos Carajás (Whitney 3 ISL, Zimmer 2 ISL), Caxiuana (Marantz 1 ML, Whitney 6 ISL, Whittaker 1 ISL, Zimmer 13 ISL), Reserva Indígena Kayapó (Whitney 1 ISL), Paragominas (Whitney 5 ISL), Fazenda Rio Capín (Zimmer 6 ISL); Tocantins: Babaculândia (Pacheco 1 ISL).
ABSTRACT.—Antbirds (Thamnophilidae) are a diverse component of neotropical forest avifaunas, and are particularly vulnerable to population declines and extirpations in fragmented landscapes. We lack estimates of apparent survival and dispersal for the majority of species, despite their value in effectively managing populations of understory birds. We studied a population of Chestnut-backed Antbird (Myrmeciza exsul) from 2004 to 2009 in a large rain forest preserve in northern Costa Rica to generate estimates of apparent annual survival (ϕ), and breeding dispersal (i.e., movement from one breeding territory to another) in continuous forest. Estimates of ϕ (± SE) of adults based on weighted model averages were high (males: 0.794 ± 0.037; females: 0.798 ± 0.050) compared to independent juveniles (males: 0.629 ± 0.159; females: 0.629 ± 0.168). Detection (recapture/reobservation) probabilities (p) were higher for males (adults: 0.916 ± 0.034; juveniles: 0.915 ± 0.049) than for females (adults: 0.544 ± 0.104; juveniles: 0.540 ± 0.115). Overall annual turnover (disappearing from the study area + territory switching) was comparable to other antbirds (~32%). Territory switching was rare, and generally limited to short movements to adjacent or nearby territories (mean distance moved = 372 m, range = 145–840 m, n = 9). Our results suggest Chestnut-backed Antbirds: (1) have relatively high adult annual survival, and (2) have limited breeding dispersal, even in a large, forested study area. Received 29 January 2010. Accepted 28 July 2010.

Accurate and precise survival estimates are important to understand life history evolution and population demography (Martin 1996, Brawn et al. 1998), and also to protect and manage tropical forest birds in fragmented landscapes (Brawn et al. 1998). The question of whether tropical forest birds survive better than their temperate counterparts has inspired considerable debate (e.g., Karr et al. 1990, Brawn et al. 1995, Johnston et al. 1997), but remains unresolved at least partially due to questions regarding methodology and phylogeny (Brawn et al. 1995, Martin 1996, Sandercock et al. 2000). Estimates of apparent survival of birds are time-consuming and logistically difficult to obtain in tropical forests, and are still lacking for the majority of tropical resident landbirds.

Blake and Loiselle (2008) summarized published estimates of apparent annual survival (ϕ) for tropical birds, including 24 species of antbirds (Thamnophilidae), a uniquely neotropical species-rich family that is particularly vulnerable to forest loss and fragmentation. They noted considerable variation in ϕ for antbirds (ϕ = 0.68; range = 0.36–0.86), likely resulting from a combination of general uncertainty in methods, genuine species differences, and possibly regional variation within species. Methodological problems are implicated as detection methods involving reobservation and recapture of color-banded birds produce higher estimates of ϕ than recapture methods alone (Blake and Loiselle 2008). A typical cost of more accurate survival estimates derived from recapture/reobservation studies is the need to focus on one or a few species due to the intensity of effort required.

The problem of estimating demographic parameters such as survival of tropical birds is exacerbated by loss and fragmentation of forests, because demography is likely altered (Karr 1990). Patterns of species loss and decline in tropical fragmented landscapes are relatively well described (e.g., Stouffer and Bierregaard 1995, Sekercioglu et al. 2002, Sodhi et al. 2004) compared to demographic mechanisms. Understory insectivores are particularly susceptible to landscape effects of deforestation and habitat fragmentation (Stouffer et al. 2006, Ferraz et al. 2007, Stouffer and Bierregaard 2007) for reasons that are not clear (Turner 1996, Soderstrom 1999). The relevant mechanisms of declines have been difficult to identify, as studies using only presence-absence or relative abundance data cannot distinguish among different factors (e.g., decreased adult survival, increased nest predation, decreased dispersal).

Forest-dwelling antbirds are particularly vulnerable to declines and extirpations in fragmented landscapes (e.g., Ferraz et al. 2007, Stouffer and Bierregaard 2007, Van Houtan et al. 2007). A growing body of evidence suggests that non-forest impedes movements for many antbird species
Compared to estimates of apparent survival, few studies exist on natural movements of antbirds, and understory insectivores in general. Nearly all studies of antbird movements have focused on breeding (as opposed to natal) dispersal (sensu Greenwood and Harvey 1982), because marking and following sufficient numbers of nestlings is logistically difficult in forest species with cryptic nests, long breeding seasons, and low nest success rates. Breeding dispersal has often been quantified in terms of territory-switching, because most species defend territories year-round. Previous studies of antbirds show: (1) annual survival of antbirds is typically relatively high compared to similar-sized temperate birds (Blake and Loiselle 2008), (2) movements by territorial individuals may occur regularly, but on a small scale (within a few territory-widths; Greenberg and Gradwohl 1997, Morton et al. 2000, Fedy and Stutchbury 2004), and (3) territory locations and boundaries within non ant-following species are fairly constant over time (Greenberg and Gradwohl 1986, Morton et al. 2000).

We studied a population of Chestnut-backed Antbirds (Myrmeciza exsul) in northern Costa Rica from 2004 to 2009 to estimate survival rates and to characterize breeding dispersal. Our objectives were to: (1) generate estimates of apparent annual survival and detection probability, and (2) quantify between-year turnover and territory switching behavior within a large forest preserve.

**METHODS**

**Study Area.**—We conducted this study in the Caribbean lowlands of northern Costa Rica, which were essentially completely forested prior to 1950 (Joyce 2006), but have become increasingly fragmented, largely by agricultural land uses. The La Selva Biological Reserve (hereafter “La Selva”) is a largely forested lowland preserve (35–137 m asl; McDade and Hartshorn 1994) in Heredia Province, encompassing >1,100 ha of old-growth tropical wet forest. La Selva is currently surrounded on three sides by a largely agricultural matrix. Annual rainfall is nearly 4,000 mm with a predictable dry season from February to April, and a less pronounced dry season from September to October (Sanford et al. 1994).

The natural history of the Chestnut-backed Antbird is summarized by Woltmann et al. (2010). Individuals are paired and maintain territories year-round, and are highly sedentary, at least at short (≤1 year) time scales (Marcotullio and Gill 1985, Stutchbury et al. 2005, Losada-Prado 2009). Moore et al. (2008) provided evidence of poor dispersal by this species by demonstrating its inability to sustain flight for 100 m over water, although how this limitation applies to dispersal in more typical terrestrial settings is unknown.

**Field Procedures.**—We selected a 300-ha focal study area (200 ha from 2004 to 2005; 300 ha from 2006 to 2009) dominated by old-growth forest (two territories included in survival analyses were outside the focal plot, but in similar habitat). Forty of 41 territories monitored were in forest at least 40 years of age with a well developed canopy and understory; the other territory was in older second-growth with a canopy height of ~3 m. Birds were lured into mist nets using conspecific playback, uniquely banded with a numbered aluminum band and three colored plastic leg bands, and released. Bird capture and marking began in December 2004, and annual dry-season surveys were conducted February–March 2005–2009 (and into Apr 2009).

Chestnut-backed Antbirds in post-juvenal plumages are readily identified as male or female based on underpart coloration (Wolfe et al. 2009). Incomplete knowledge of the timing of definitive prebasic molt and observations of breeding activity nearly year-round at La Selva indicate that Hatch-Year (HY) and After-Hatch-Year (AHY) terminology is inappropriate at this site. We classified birds as “adult” (fully ossified skull and definitive plumage) or “juvenile” (skull <90% ossified or formative plumage; Howell et al. 2003), and note we occasionally captured “juvenile” birds in breeding condition (cloacal protuberance and/or brood patch).

We attempted to relocate all previously marked birds during each annual survey, and to capture any unbanded individuals. Territories were thoroughly searched during morning hours with good weather (when birds are most active and vocal), and vocalization playback was used to find and identify individuals. We considered a territory unoccupied if no bird was found after two separate searches (minimum 45 min each) at least
3 days apart. Chestnut-backed Antbirds have relatively small territories, respond readily to playback, and are most responsive to dry-season playback, making it unlikely we incorrectly declared a territory unoccupied.

Data Analyses.—We used Program MARK, Version 5.1 (White and Burnham 1999) to evaluate Cormack-Jolly-Seber (CJS) models of apparent survival (c) and detection (reobservation or recapture) probability (p) of territorial birds, and to generate parameter estimates of survival and detection probability. Models were constructed to examine effects of age (juvenile vs. adult) and males or females on estimates of c and p, and were ranked using AICc values. We had no a priori reason to expect year effects, nor did we have sufficient data to test for them after individuals were grouped into age and male/female classes. We used U-CARE Version 2.2 (Choquet et al. 2005) to test the most parameterized model for evidence of transience and trap-dependence. We used the median c approach in MARK to test goodness-of-fit of a general model to ascertain whether adjustments to model rankings were necessary. The first capture interval in our data set was 0.25 (Dec 2004 to Feb 2005), but all subsequent intervals were set to one. We considered the best supported models as those with ΔAICc < 2, and used AICc-weighted model averaging (over all models) to derive estimates of c and p in MARK.

There were 111 detection events involving 77 individuals (54 males and 23 females). The U-CARE analysis indicated no significant problems of transience (P = 0.290) or trap-shyness (P = 0.464). Data were too sparse in some age-sex classes to evaluate a fully time-dependent model. A goodness-of-fit test on the next most parameterized model, \{c | age*sex p | age*sex\} produced an estimated median c of 0.991 (SE = 0.018), not meaningfully different from 1, and no adjustments to model rankings were made.

We describe annual territory dynamics of Chestnut-backed Antbirds following Greenberg and Gradwohl (1997) and Fedy and Stutchbury (2004), and include only territories within the 300-ha focal plot. Annual turnover includes all changes in territorial positions (i.e., birds that disappeared from the study area plus birds known to have switched territories). Both turnover and switching are presented in terms of “territory-years” (i.e., a marked bird monitored from 1 year to the next), calculated separately for males and females; these are minimum estimates of turnover and switching (Morton et al. 2000).

RESULTS

Apparent Survival and Detection Probability.—The two best models (ΔAICc < 2) indicated differential detection of males and females, but differed in whether or not c varied by age (Table 1). Estimates of c ± SE of adults based on weighted model averaging were relatively high (males: 0.794 ± 0.037; females: 0.798 ± 0.050) compared to estimates of c for independent juveniles (males: 0.629 ± 0.159; females: 0.629 ± 0.168; Fig. 1). Detection probabilities were higher for males (adults: 0.916 ± 0.034; juveniles: 0.915 ± 0.049) than for females (adults: 0.544 ± 0.104; juveniles: 0.540 ± 0.115).

### Table 1: Models of apparent survival (c) and detection probability (p) of Chestnut-backed Antbirds at La Selva, Costa Rica

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weights</th>
<th>Model likelihood</th>
<th># Par</th>
<th>Deviance</th>
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<tr>
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<td>275.306</td>
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<td>4.128</td>
<td>0.085</td>
</tr>
<tr>
<td>{c</td>
<td>p</td>
<td></td>
<td>}</td>
<td>290.485</td>
<td>4.128</td>
<td>0.085</td>
</tr>
<tr>
<td>{c</td>
<td>p</td>
<td></td>
<td>}</td>
<td>290.485</td>
<td>4.128</td>
<td>0.085</td>
</tr>
<tr>
<td>{c</td>
<td>p</td>
<td></td>
<td>}</td>
<td>290.485</td>
<td>4.128</td>
<td>0.085</td>
</tr>
<tr>
<td>{c</td>
<td>p</td>
<td></td>
<td>}</td>
<td>290.485</td>
<td>4.128</td>
<td>0.085</td>
</tr>
</tbody>
</table>
Estimates of \( \varphi \) were similar for all adults, but estimates of \( \varphi \) for juveniles were not informative due to large 95% confidence intervals (Fig. 1A). Detection probability differed markedly between males and females with females being detected less frequently once marked (Fig. 1B).

**Territory Dynamics.**—Seventy-two banded individuals (51 males, 21 females) were followed for at least 1 year within the 300-ha focal plot for a total of 160 territory-years (Table 2). False disappearance rate of males and females differed (2 and 6 instances for males and females, respectively), and we adjusted overall turnover rates. Turnover was similar between males and females, and was dominated by disappearances (86%) as opposed to switching (14%; Table 3). Turnover was slightly higher for juveniles. We found no evidence of differential switching rate between males and females (\( X^2 = 0.115, df = 1, P = 0.73 \)), but our small sample size of switching resulted in low statistical power.

We documented nine cases of territory switching (4 females, 4 males; one male switched twice). The mean (± SE) distance moved was 372 ± 124 m (range = 145–840), and did not differ between males and females (ages pooled, \( t = 0.466, df = 7, P = 0.655; \bar{x} = 334 \) and 420 m for males and females, respectively). Juveniles tended to move greater distances (all pooled; \( t = 2.182, df = 7, P = 0.065; \bar{x} = 590 \) and 263 m for all juveniles and all adults, respectively). Five of the nine cases involved switching to adjacent territories; the greatest distance moved was by a juvenile female. Results were similar when analyzed in terms of territory-widths (≈163 m). Genetic parentage analysis revealed that none of the juveniles in our analyses was the offspring of the social mate (Woltmann 2010); we detected no instances of juveniles inheriting the natal territory. Undetected switches involving longer distances outside the study area likely occurred, but our focal plot size (300 ha) and dimensions (the most distant territories were >2 km apart) suggest that we could have detected greater movements than the mean distance of <400 m.

Four occupied territories became vacant over
TABLE 2. Number (sample size) of territory-years (T-Y), observed disappearances and switches, and adjusted disappearance rates for Chestnut-backed Antbirds in Costa Rica. $D_{\text{obs}}$ = observed disappearance rate; $D_{\text{err}}$ = false disappearance rate, calculated for 2005-2008, and $D_{\text{adjusted}} = D_{\text{obs}} - D_{\text{err}}$ which was used in place of $D_{\text{obs}}$ in turnover calculations (Table 3).

<table>
<thead>
<tr>
<th>Gender</th>
<th>T-Y</th>
<th>Obs. (#) disappeared</th>
<th>Obs. (#) switched</th>
<th>$D_{\text{obs}}$</th>
<th>$D_{\text{err}}$</th>
<th>$D_{\text{adjusted}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>100</td>
<td>26</td>
<td>4</td>
<td>0.260</td>
<td>0.014</td>
<td>0.246</td>
</tr>
<tr>
<td>Juvenile</td>
<td>15</td>
<td>6</td>
<td>1</td>
<td>0.400</td>
<td>0.083</td>
<td>0.317</td>
</tr>
<tr>
<td>All</td>
<td>115</td>
<td>32</td>
<td>5</td>
<td>0.278</td>
<td>0.024</td>
<td>0.255</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>36</td>
<td>16</td>
<td>3</td>
<td>0.444</td>
<td>0.185</td>
<td>0.259</td>
</tr>
<tr>
<td>Juvenile</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>0.444</td>
<td>0.125</td>
<td>0.319</td>
</tr>
<tr>
<td>All</td>
<td>45</td>
<td>20</td>
<td>4</td>
<td>0.444</td>
<td>0.171</td>
<td>0.273</td>
</tr>
</tbody>
</table>

the course of our study, but four previously unoccupied territories became occupied (one gain resulted from a territory splitting). Between three and six once-occupied territories were empty in any given year, and density was relatively stable at 9.3–10.0 pairs/100 ha from 2006 to 2009. Territory locations and boundaries appeared stable regardless of the owner, suggesting territory locations are intrinsic to the environment, or become constrained by traditional boundaries.

We identified seven males and one female (the female was not captured) on the 300-ha focal plot that appeared to be floaters. These were generally (6 of 8) unpaired individuals that responded

TABLE 3. Annual turnover and territory switching of Chestnut-backed Antbirds compared to ecologically similar species. Numbers in columns represent males and females respectively, where available; a single value represents males and females combined.

<table>
<thead>
<tr>
<th>Species</th>
<th>Turnover</th>
<th>Switch rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Chestnut-backed Antbird</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>0.29</td>
<td>0.34</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.39</td>
<td>0.43</td>
</tr>
<tr>
<td>All</td>
<td>0.30</td>
<td>0.36</td>
</tr>
<tr>
<td>Spotted Antbird (Hylophylax naevioides)</td>
<td>0.27</td>
<td>0.32</td>
</tr>
<tr>
<td>Bicolored Antbird (Gymnopithys leucopsis)</td>
<td>0.39</td>
<td>0.53</td>
</tr>
<tr>
<td>Ocellated Antbird (Phaenostictus mcleannani)</td>
<td>0.26</td>
<td>0.49</td>
</tr>
<tr>
<td>Checker-throated Antwren (Epinecrophylla fulviventris)</td>
<td>~0.33</td>
<td></td>
</tr>
<tr>
<td>Dusky Antbird (Cercomacra tyrannina)</td>
<td>0.23</td>
<td>0.25</td>
</tr>
<tr>
<td>White-bellied Antbird (Myrmeciza longipes)</td>
<td>0.36</td>
<td>0.36</td>
</tr>
<tr>
<td>Buff-breasted Wren (Caniochilus leucotos)</td>
<td>0.07</td>
<td>0.15</td>
</tr>
</tbody>
</table>

* Estimated separately for a subset of contiguous territories (E. S. Morton, pers. comm.).
* Averaged over 3 years, derived from Gill and Stutchbury (2006: Table 1).
aggressively to playback, but were not associated with a known territory. Three (2 juveniles) of the floater males (4 juveniles, 3 adults) were seen again elsewhere on the plot in subsequent years with females on known territories. One juvenile male traveled through the focal plot with an unbanded female in 2006 and attempted to establish a territory in the center of the study area, but both birds disappeared within 1 week. This “territory” had not been previously occupied, and was not occupied thereafter.

DISCUSSION

Chestnut-backed Antbirds, once on a territory, exhibit restricted movement. The few individuals that switched territories typically moved to an adjacent territory, and all movements observed were <850 m. Mean life span of adult Chestnut-backed Antbirds at La Selva is ~4.24 years (mean life span = 1/−ln(s), where s = annual survival; Brownie et al. 1985). Thus, breeding dispersal, even over the course of a lifetime, may be insufficient to maintain direct demographic or genetic connectivity between populations separated by more than a few kilometers, especially if barriers (e.g., large rivers, habitat discontinuities) are present.

**Apparent Annual Survival and Detection Probability.**—Our estimates of p for adult Chestnut-backed Antbirds are at the high end of the range of estimates for other thamnophilids summarized by Blake and Loiselle (2008) (range = 0.45–0.87). We found no evidence for differential apparent survival between adult males and females, and high detection probabilities suggest that our estimates of p are close to true survival, at least for adult males (Jones et al. 2004, Ruiz-Gutiérrez et al. 2008). Apparent survival of all juveniles was poorly estimated largely due to small sample size, as juveniles by definition only contribute to a single capture period, and afterwards contribute to adult survival estimates. However, p for juvenile males was relatively high, and the large confidence intervals around estimates of juvenile male survival can be interpreted as evidence of greater variability in apparent survival.

Detection probabilities (p) of males and females were strikingly different with females having lower and more variable values. The unequal detection rates of age and male or female classes highlight ecologically important differences in the behavior of individuals (e.g., Crespin et al. 2008), and also have methodological implications. For example, in sexually monomorphic species, or those with delayed male plumage maturation (e.g., some Pipridae; DuVal 2005), important differences in apparent survival among groups may go undetected, and lead to high variance of parameter estimates.

**Turnover Rate and Territory Switching.**—Overall rate of turnover (disappearing + switching) by Chestnut-backed Antbirds at La Selva was comparable to other antbird species. Turnover was higher for females, and turnover among female Chestnut-backed Antbirds was the highest reported for any species (Table 3). Territory switching by Chestnut-backed Antbirds was markedly less common than for several other species studied (e.g., White-bellied [Myrmeciza longipes] and Dusky [Cercomacra tyrannina] antbirds). The few territory switches of Chestnut-backed Antbirds observed generally were on the scale of 1–2 territory-widths, and all switches involved distances of <1 km, consistent with patterns in other small tropical understory resident insectivores (Greenberg and Gradwohl 1997, Morton et al. 2000, Robinson 2000, Gill and Stutchbury 2010). Low switching rates and short breeding dispersal distances have been reported in a wide variety of bird species, both tropical and temperate, and may be a general characteristic of monogamous species with year-round, multipurpose territories (e.g., Woolfenden and Fitzpatrick 1989, Bried and Jouventin 1998, Komdeur and Edelaar 2001, Thorstrom et al. 2001, VanderWerf 2004, Gill and Stutchbury 2006, Eikenaar et al. 2008, Gill and Stutchbury 2010).

The abundance of floaters (sensu Winker 1998) is difficult to quantify, especially for females. Most territorial vacancies (male and female) were filled from year to year, mainly by unbanded birds, and both adults and juveniles were represented among the replacements. However, not all vacancies were filled, and some territories remained vacant at the end of our study. How floaters may affect long-term population trends or estimates of dispersal patterns is not clear, but should be considered in future studies (Zack and Stutchbury 1992, Winker 1998).

CONSERVATION IMPLICATIONS

Our findings have important implications for conservation of tropical understory forest birds in fragmented landscapes. Rare and small-scale lifetime breeding dispersal by Chestnut-backed Antbirds in a contiguous forest setting agrees with
other studies documenting breeding dispersal patterns in tropical birds (Greenberg and Gradwohl 1997, Morton et al. 2000, Fedy and Stutchbury 2004). Short movements through continuous and favorable rain forest habitat (Losada-Prado 2009, this study), coupled with inability to fly long distances (Moore et al. 2008) makes breeding dispersal between forest fragments separated by kilometers of unsuitable habitat unlikely in this and perhaps other ecologically similar species (Woltmann 2010).

Knowledge of genetic and demographic connectivity is needed to understand why some species persist in highly fragmented landscapes and others do not. Chestnut-backed Antbird nests are difficult to find, and breeding activity by this species occurs nearly year-round at La Selva, necessitating intense (essentially year-round) field effort to find and monitor sufficient nests. Moreover, clutch size is low in this and many other tropical understory species (Skutch 1985), post-fledging parental care is often extensive (Russell et al. 2004), all of which increase the amount of effort required to track fledglings or otherwise measure natal dispersal. These technical and logistic difficulties suggest that alternate methods (e.g., molecular genetic approaches) are needed to complement field-based approaches to understanding demographic and genetic connectivity in complex landscapes.

ACKNOWLEDGMENTS

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GREENBERG, R. AND J. GRADOVOHL. 1997. Territoriality, adult survival, and dispersal in the Checker-throated

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ORNITHOLOGICAL RECORDS FROM A CAMPINA/CAMPINARANA ENCLAVE ON THE UPPER JURUÁ RIVER, ACRE, BRAZIL

EDSON GUILHERME1,2,4 AND SÉRGIO H. BORGES3,4

ABSTRACT.—We inventoried the bird fauna of an isolated enclave of white-sand vegetation, known locally as a campina/campinarana, in the western extreme of the Brazilian State of Acre between 22 and 31 January 2007 (wet season). A total of 114 bird species was registered in 1,425 net-hrs of mist-netting and 8 hrs of recordings of vocalizations. This included six species known to be associated with campinas and campinaranas in western Amazonia. A number of important records were made of species endemic to the southwestern Amazon Basin, but poorly-known in Brazil. Despite the relatively small size of the campina/campinarana enclave, these records indicate the area is extremely important for conservation of local biodiversity, and reinforces the need for further studies of both the avifauna and other groups of animals. Received 4 March 2010. Accepted 6 August 2010.

Campina and campinarana refer to a complex mosaic of non-forest vegetation growing on nutrient-poor sandy soils at a number of different locations throughout the Amazon Basin (Anderson 1981, Daly and Mitchell 2000, Alonso and Whitney 2003, Vicentini 2004). These two types of habitat are most common in the basin of the Rio Negro, which is a major northern (left bank) tributary of the Amazon/Solimões River (Macedo and Prance 1978, Hess et al. 1998). Local residents in Brazil use campina to refer to “islands” or enclaves of bushy herbaceous vegetation on white-sand soils, which form patches of open grassland in the middle of the forest. Residents refer to this habitat as campinarana, which means “false campina”, when the vegetation of these enclaves is characterized by relatively high densities of trees of reduced stature and girth, but lacks emergents, lianas, or epiphytes (Anderson 1981). Campinas and campinaranas are found only in the western extreme of the State of Acre in the River Juruá Basin (Acre 2000, IBGE 2005).

The species richness of the flora of the campinaranas is relatively low in comparison with other forested ecosystems in the Amazon, but botanical research in these enclaves has revealed a relatively large number of endemic species (Anderson 1981, Daly and Mitchell 2000, Vicentini 2004). A similar pattern of high levels of endemism has been recorded in studies of invertebrate (Höfer et al. 1996, Marini-Filho 1999, Barbosa et al. 2002, Ricetti and Bonaldo 2008) and vertebrate (e.g., birds: Oren 1981, Alonso 2002, Alonso and Whitney 2003, Borges 2004, Poletto and Aleixo 2005) faunas of campina and campinarana enclaves. Species richness and abundance are markedly lower than those of the adjacent forest ecosystems.

Birds are the best-studied vertebrate group from the white-sand enclaves of the Amazon. Surveys at a number of sites have revealed new species (Whitney and Alonso 1998, Alonso and Whitney 2001, Isler et al. 2002) and expanded the known geographic ranges of a number of taxa (Borges and Almeida 2001, Alonso and Whitney 2003, Poletto and Aleixo 2005). Borges (2004) argued that comparisons between bird communities from different Amazonian campinas are hindered by a lack of inventories for most sites.

We provide the first discussion and annotated list of the bird fauna of a campina/campinarana enclave on the upper Rio Juruá in the Brazilian State of Acre. This enclave is isolated from all others in southwestern Amazonia.

METHODS

Study Area.—The campina/campinarana enclave studied is in the municipality of Porto Walter, on the right bank of the stream Cruzeiro do Vale (08° 20' 35.7" S, 72° 36' 19.7" W, Fig. 1). The enclave has a total area of 103 km² and is 193 m above sea level. It is bordered by both várzea (flooded whitewater habitat) and terra
The survey of the bird fauna occurred between 22 and 31 January 2007. Edge habitats bordering the surrounding várzea and terra firme forests were also sampled. A base camp was established at the Colônia Dois Portos community on the bank of the Cruzeiro do Vale stream, ~2 km from the campina enclave. The community was inhabited by 20 people in four families. The area surrounding the base camp included a small pasture for cattle and a tract of secondary forest (regenerating from subsistence agriculture), where additional observations of birds were conducted.

Species Inventory.—The local bird fauna was inventoried using two procedures: (1) quantitative sampling through captures with 20, 12 \times 2\text{-m mist nets (36 mm mesh), and (2)} collection of complementary records based on field observations with 8 \times 42 binoculars and recordings of vocalizations using a Sony TCM 5,000 recorder. Mist nets were set in linear transects of 10 nets each within the campina and campinarana, and in the adjacent forest edge. Nets were set at dawn (0530 hrs) and remained open until 1500 hrs to maximize the number of specimens captured. Voucher specimens were collected for laboratory analysis. All specimens were prepared using standard taxidermy techniques and deposited in the Ornithology Laboratory of the Goeldi Museum (Museu Paraense Emílio Goeldi-MPEG) in Belém. Specimen collection was authorized by the Brazilian Environment Institute (IBAMA), through license number 044/2006-COFAN. Scientific nomenclature followed that recommended by the IOC (Gill and Donsker 2010).

RESULTS AND DISCUSSION

The 10 days of data collection resulted in 1,425 net/hrs of captures using mist nets, and 8 hrs of recordings resulting in identification of 114 species of birds (Table 1). Six (4.4\%) are known to be associated with campinas and campinaranas of the western Amazon (Stotz et al. 1996, Alonso 2002). Only two, Zimmer’s Tody-Tyrant (*Hemiprincus minimus*) and Black Manakin (*Xenopipo atronitens*) are included in Stotz et al.’s (1996) list of birds associated with the white-sand habitats of the southern Amazon Basin. We also report important records of species endemic to southwestern Amazonia but which are little known in Brazil (Guilherme and Borges 2008).

Brown-banded Puffbird (*Notharchus ordii*). This species is often associated with habitats on white sandy soils in northeastern Peru (Alonso
TABLE 1. Avian families and species recorded in campina and campinarana habitats in western Acre. Habitat: CA = Campina; CN = Campinarana; RF = riparian forest; OF = Open rain forest with palms; FE = forest edge; SF = secondary forest. Records: S = specimen collected and deposited at the Goeldi Museum; O = observation; V = vocalization recorded and recognized.

<table>
<thead>
<tr>
<th>Family (number of species)</th>
<th>Species</th>
<th>Habitat</th>
<th>Record</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tinamidae (3)</td>
<td>Tinamus guttatus</td>
<td>CN, OF</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Crypturellus undulatus</td>
<td>CN, OF</td>
<td>S, V</td>
</tr>
<tr>
<td></td>
<td>C. strigulosus</td>
<td>CN</td>
<td>V</td>
</tr>
<tr>
<td>Ardeidae (1)</td>
<td>Butorides striata</td>
<td>RF</td>
<td>S, O</td>
</tr>
<tr>
<td>Accipitridae (2)</td>
<td>Elanoides forficatus</td>
<td>FE</td>
<td>O</td>
</tr>
<tr>
<td></td>
<td>Harpagus bidentatus</td>
<td>OF</td>
<td>S</td>
</tr>
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<td>Psophiidae (1)</td>
<td>Psophia leucoptera</td>
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<td>Eurypga helias</td>
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<td>S, O</td>
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<td>Leptotila verreauxa</td>
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<td>S</td>
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<tr>
<td></td>
<td>L. rufaxilla</td>
<td>CA, OF</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Geotrygon montana</td>
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<td>S</td>
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<td>C. major</td>
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<td>S, O</td>
</tr>
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<td>Strigidae (1)</td>
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<td>S</td>
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<td></td>
<td>Topaza pyra</td>
<td>CA</td>
<td>S</td>
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<tr>
<td></td>
<td>Chrysauronia oenone</td>
<td>FE, RF</td>
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<td></td>
<td>Heliomaster longirostris</td>
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<td>Trogonidae (3)</td>
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<td>S, O</td>
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<td>S, O</td>
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<td>Bucco macrodactylus</td>
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<td></td>
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<td>S</td>
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<td></td>
<td>Colaptes punctigula</td>
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<td>S, O, V</td>
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<tr>
<td></td>
<td>Picaeus chrysochlorus</td>
<td>CN</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Celeus elegans</td>
<td>OF</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>C. grammicus</td>
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<td>S</td>
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<tr>
<td>Thamnophilidae (13)</td>
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<td>S</td>
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<td>Taraba major</td>
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<tr>
<td></td>
<td>T. maruni</td>
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*Species closely associated with campina and campinarana habitats of southwestern Amazonia (Stotz et al. 1996, Alonso 2002).*

and Whitney 2003), southwestern Venezuela, and the upper Rio Negro region of northern Brazil (Zimmer and Hilty 1997). The first record of this species in Acre was from Serra da Jaquirana, in dense submontane rain forest, in Serra do Divisor National Park. Two specimens were collected and deposited in the Goeldi Museum collection (Alonso and Whitney 2003: MPEG 52726, 52727). The female we collected (MPEG 62025) in *terra firme* forest at the edge of the campinarana on 26 January 2007, represents the second record of this species for Acre.

Fiery Topaz (*Topaza pyra*). This species is widely distributed in the western Amazon Basin, including Brazil, Peru, and Ecuador (Hu et al. 2000), but is known from Acre only from three specimens collected by D. C. Oren and coworkers in Serra do Divisor National Park (MPEG 52719, 52720, 52721). We collected a male (MPEG 62008) on 24 January 2007 in a mist net in open campina habitat. This record represents the southernmost limit of the distribution of the species in the Amazon biome. Our record does not support the hypothesis that distribution of Fiery Topaz in southwestern Amazonia is related to blackwater river basins, as suggested by Hu et al. (2000). The drainage of our study area is exclusively whitewater, characterized by high concentrations of suspended sediments (Toivonen et al. 2007) in contrast with the region of Cruzeiro do Sul (where the first Acre records of Fiery Topaz were collected) which, near Serra do Moa, is dominated by blackwater streams (EG, pers. obs.). The Fiery Topaz has been recorded frequently in campinarana habitats, including Jaú National Park (Borges et al. 2001) and the municipality of Guajará in Amazonas State (A. Aleixo, unpubl. data). We believe the distribution of Fiery Topaz, in contrast with that of its congener Crimzon Topaz (*T. pella*), is more closely related to campina and campinarana habitats than blackwater river basins.

Golden-tailed Sapphire (*Chrysuronia oenone*). The first published record of this species from Brazil was provided by Ruschi (1957) based on two specimens collected by D. C. Oren and co-workers in Serra do Divisor National Park (MPEG 52719, 52720). There are only two additional Brazilian records, both from the upper Rio Jurua in Acre. One record is from the Alto Jurua Extractive Reserve (Whittaker et al. 2002), and the other is from Serra do Divisor National Park (B. M. Whitney, unpubl. data; Guilherme 2009). The species appears to be common in the várzea habitats of the Juruá Basin. The species was observed on a daily basis at our study site, feeding on *Inga* spp. inflorescences in the várzea forest adjacent to the campinarana. A male (MPEG 62006) was collected on 31 January 2007 in the várzea forest outside a school next to our base camp. This is the first specimen from Acre.

Antbird (*Myrmeciza* spp.). We collected a male (MPEG 62088) on 24 January 2007 belonging to the Southern Chestnut-tailed Antbird (*M. hemimelaena*) species complex, in *terra firme* forest at the edge of the campinarana. EG compared the specimen with 35 others in Museu Goeldi’s ornithological collection, collected at a variety of localities in Acre (Guilherme 2009), and noted the pileum was distinctly blackish in contrast with the gray of those of other specimens of Chestnut-tailed Antbird. This pattern was also observed in a male (MPEG 57134) collected in Tefé, Amazonas, a region with abundant campinarana habitat. The black pileum in these two specimens appears to agree with Zimmer’s (1932) description of a male Zimmer’s Antbird (*M. hemimelaena castanea*) from Loreto, northwestern Peru. Isler et al. (2002) recently elevated this form to full species status, based on an analysis of morphological
traits and vocalization patterns. We decided against classifying the MPEG 62088 specimen as Zimmer’s Antbird (M. castanea) because we believe a more thorough investigation of the Goeldi Museum specimens collected in campinaranas of the southwestern Amazon Basin is necessary. A more detailed field study of the ecology and vocalizations of individuals with these morphological traits is also necessary. This would permit more reliable comparisons with the characteristics of the Peruvian Zimmer’s Antbird (Isler et al. 2002), and a more dependable identification of the specimen collected in the present study.

Amazonian Barred Woodcreeper (Dendrocolaptes certhia polyzonus). The most common form of this taxon in Acre is D. c. juruanus, which has been recorded throughout practically the entire state (Pinto and Camargo 1954, Novaes 1957, Guilherme 2009). We netted four Amazonian Barred Woodcreepers between 23 and 27 January 2007 in the campinarana, three of which were collected—one female (MPEG 62042) and two males (MPEG 62043–62044). EG concluded, upon analyzing specimens in the Museu Goeldi’s ornithological collection, that these individuals have more striking coloration, including well-defined black striping of the pileum, mantle, and throat, which is conspicuously different when compared with the other specimens of D. c. juruanus collected in Acre. The plumage traits of the specimens collected in the campinarana during the present study appear to coincide with those observed in D. c. polyzonus from the southwestern edge of Amazonia, Bolivia and Peru (Marantz et al. 2003; R. Batista and A. Aleixo, unpubl. data). This record of D. c. polyzonus from Acre is the first for Brazil.

Citron-bellied Attila (Attila citriniventris). This species is uncommonly documented in southwestern Amazonia with the majority of specimen records from northern Peru (Robbins et al. 1991, Schultenberg et al. 2007). The Citron-bellied Attila has been recorded in forested habitats in Acre on the upper Jurú by Whittaker et al. (2002), and A. Aleixo and F. Poletto (unpubl. data). We collected two specimens on 22 and 23 January 2007, a female (MPEG 62124) and a male (MPEG 62125), in the campinarana. This species can also be found in terra firme forest (Robbins et al. 1991), but we believe it is more closely associated with campinarana habitats than rain forest (Alonso 2002, Schultenberg et al. 2007), as observed at our study site, and in Juá National Park north of the Rio Solimões (Borges et al. 2001).

Zimmer’s Tody-Tyrant (Hemitriccus minimus). This species is patchily distributed in the Amazon Basin (Fitzpatrick et al. 2004). It occurs in igapó forests in the Rio Negro Basin (Novaes 1994, Borges et al. 2001) and in terra firme forest in Mato Grosso (Zimmer et al. 1997), but this species appears in many areas to be closely associated with campinarana habitats (Stotz et al. 1996, Borges et al. 2001, Alonso 2002, Alonso and Whitney 2003, Fitzpatrick et al. 2004). We collected a male (MPEG 62117) in the campinarana on 23 January 2007. Zimmer’s Tody-Tyrant has also been recorded in a campina/campinarana enclave in the municipality of Guajará, Amazonas, close to the city of Cruzeiro do Sul in Acre (A. Aleixo, unpubl. data) and in a bamboo (Guadua spp.) forest in eastern Acre (Guilherme and Santos 2009).

Fuscous Flycatcher (Cnemotriccus fuscatus duidae). This taxon has only been recorded in western Acre (Guilherme 2009). We collected a male and a female C. f. duidae (MPEG 62119 and 62175, respectively) in the campinarana on 22 and 24 January 2007. We believe C. f. duidae in Acre is a facultative inhabitant of the campina and campinarana formations, given that it has also been recorded in other habitats, including submontane forests of Serra do Divisor National Park, in the western extreme of the state (B. M. Whitney, unpubl. data; MPEG 52797). Alonso (2002) suggests C. f. duidae is better treated as a distinct species (Cnemotriccus duidae) given differences in plumage, vocalizations, and habitat preferences compared to those of other taxa in the complex. He noted that a taxonomic revision of the C. fuscatus complex is in preparation by B. M. Whitney and collaborators.

Black Manakin (Xenopipo atronitens). This species is an Amazonian white-sand habitat specialist (Oren 1981, Stotz et al. 1996, Borges 2004, Poletto and Aleixo 2005, Schultenberg et al. 2007). The recorded localities closest to Acre are “Pampas del Heath” on the Bolivian border in southeastern Peru (Graham et al. 1980), and a campinarana enclave in the municipality of Guajará in southwestern Amazonas on the border with Acre (Poletto and Aleixo 2005). Thirteen individuals were captured in mist nets set in the campinarana between 22 and 31 January. Six were collected (MPEG 62141–62146; 4 males, 2
I not only birds, but also other taxonomic groups, to need for further studies in this region, including forests adjacent to this enclave. We emphasize the that are poorly-known in Brazil are found in the Amazonia. In addition, a number of bird species dispersed and patchily distributed in southwestern present study is relatively small. However, it supports habitat specialists which are widely-

Yellow-green Vireo (Vireo flavoviridis). This is a Nearctic-neotropical migrant rarely observed in Brazil (Whitney and Pacheco 2001). All Brazilian records of this species with the exception of the specimens collected by J. Hidasi on the Rio Javari in Amazonas State (Whitney and Pacheco 2001), are from Acre (Whittaker and Oren 1999, Guilherme 2009). We collected one bird (MPEG 62172) on 27 January 2007 in secondary forest adjacent to the campinarana. This is the first specimen of this taxon collected in Acre, and only the fourth from Brazil. EG subsequently, on 17 November 2007, collected another specimen of Yellow-green Vireo in várzea forest on the left bank of the Rio Envira in central Acre. These records indicate the species can be found throughout the State of Acre, at least during the North temperate winter, between November and March.

Casqued Oropendola (Clypicteris oseryi). This species was recorded in Brazil first by Whittaker and Oren (1999) in the Jurua Basin (Amazonas and Acre). There are now a number of records of this species from Acre (Guilherme 2009), including some from the eastern extreme of the state (A. Aleixo and E. Guilherme, unpubl. data). We collected two specimens (MPEG 62208, 62209) on 30 January 2007 in várzea forest on the left bank of the Cruzeiro do Vale stream, adjacent to our base camp.

The campinarana enclave surveyed in the present study is relatively small. However, it supports habitat specialists which are widely-
disperssed and patchily distributed in southwestern Amazonia. In addition, a number of bird species that are poorly-known in Brazil are found in the forests adjacent to this enclave. We emphasize the need for further studies in this region, including not only birds, but also other taxonomic groups, to demonstrate the need for establishment of a permanently protected area by local authorities within the near future.

ACKNOWLEDGMENTS

The authors are grateful to Conservation International (CI–Belém) for financial support of the expedition to the campinaranas of western Acre through the project “Bird Fauna of the State of Acre: Composition, Geographic Distribution, and Conservation”. We thank Alexandre Aleixo, curator of the ornithological collection of the Goeldi Museum, for technical and field support and for comments on identification of specimens in the laboratory. We are also grateful to Sr. Damião Gonçalves for permission to work in the Dois Portos colony, and to Sr. Léoncio for field assistance. We thank the renowned taxidermist Sr. Manoel Santa Brígida for dedicated and skillful preparation of specimens in the field. We also thank Alex Jahn and Kevin Zimmer for reviewing the manuscript.

LITERATURE CITED


STABLE NITROGEN AND CARBON ISOTOPES MAY NOT BE GOOD INDICATORS OF ALTITUDINAL DISTRIBUTIONS OF MONTANE PASSERINES

YUAN-MOU CHANG,1 KENT A. HATCH,2 HSIN-LIN WEI,1 HSIAO-WEI YUAN,3 CHENG-FENG YOU,4 DENNIS EGGETT,5 YI-HSUAN TU,6 YA-LING LIN,7 AND HAU-JIE SHIU1,8

ABSTRACT.—We examined δ15N and δ13C values of feathers from nine species, belonging to three feeding guilds (herbivores, omnivores, and insectivores), of wild passerines at eight sites along an altitudinal gradient (339–2,876 m asl) within Taroko National Park, Taiwan. We examined: (1) if altitudinal patterns in feather δ15N and δ13C are consistent with previously published values for plants and soils, (2) if feather δ15N and δ13C differ among sites, and (3) if there are year-to-year and/or month-to-month fluctuations in feather δ15N and δ13C of the same birds. We found no simple relationship between feather isotope values and altitude. Feather δ15N values decreased significantly with increasing altitude for insectivores, but not for herbivores and omnivores. Feather δ13C values increased significantly with increasing altitude for herbivores and omnivores, but not for insectivores. Altitudinal trends in feather δ15N and δ13C values exhibit even more inconsistent patterns when data were analyzed by species: feather δ15N and δ13C values for some species increased significantly with increasing altitude, others decreased significantly with increasing altitude, and still others exhibited no significant relationship between isotopic values and altitude. The R² for the relationship between feather δ15N, δ13C values and altitude was generally low regardless of whether the analysis was by feeding guilds or species. This indicates much of the variation cannot be explained by altitude. There were either no significant differences between sites, or significant differences between some but not all sites when investigating δ15N or δ13C, whether by feeding guilds or by species. Our study suggests that carbon and nitrogen isotopes may be not useful markers to track altitudinal migration of montane passerines. Received 16 April 2010. Accepted 15 September 2010.

Stable isotope analysis in animals is a powerful tool in reconstruction of diets (Hobson and Clark 1992), trophic levels (Kelly 2000), feeding habitats (Hobson and Scaly 1991, Cherel et al. 2000), and in understanding migration patterns (Hobson 1999b, Webster et al. 2002, Rubenstein and Hobson 2004, Hobson 2005). Feathers are particularly appealing material for use in stable isotope studies of the migratory ecology of birds because they are metabolically inert after synthesis. Isotopic signatures of both temporal and, if the animal is moving, spatial scales are, therefore, permanently recorded in the feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson 1999a, Kelly 2000, Wassenaar and Hobson 2000, Kelly et al. 2002, Rubenstein et al. 2002, Dalerum and Angerbjorn 2005). Despite the wide application of stable isotopes to questions of animal migration, the potential value for examining altitudinal migration has been little studied (Graves et al. 2002, Hobson et al. 2003, Yi and Yang 2006, Mannel et al. 2007).

Studying altitudinal migration using stable isotopes relies on variation in isotopic signatures over an altitudinal gradient. In plants, δ13C values typically increase with increasing altitude which is related to plant physiological adaptation to changes in CO2 partial pressure, soil moisture, ambient humidity, and air pressure with altitude (Korner et al. 1988, 1991; Marshall and Zhang 1994; Sparks and Ehleringer 1997). In contrast, δ15N values in plants and soil decrease with increasing altitude due to the influence of lower temperatures, lower pH, and higher precipitation at higher altitude (Mariotti et al. 1980, Schuur and Matson 2001, Amundson et al. 2003). The isotope patterns at the base of the food chain can be
passed on to the organisms at higher trophic levels, and animals should reflect the altitudinal trends of the plants and soils in their local habitats (Mannel et al. 2007).

However, not all animals exhibit altitudinal trends of δ¹³C and δ¹⁵N similar to those observed in plants and soils. Previous studies on altitudinal patterns of isotopic signatures in animals have focused on either one species (Graves et al. 2002, Yi and Yang 2006) or several species within a single feeding guild (e.g., nectarivores or herbivores) (Hobson et al. 2003, Mannel et al. 2007). In each case they were primary consumers. The δ¹³C values of animals in some cases become more positive with increasing altitude (Graves et al. 2002, Mannel et al. 2007), while others show no altitudinal trends (Graves et al. 2002). Two studies show δ¹⁵N values increase with increasing altitude (Hobson et al. 2003, Yi and Yang 2006), one study shows no altitudinal trend (Graves et al. 2002), and the other shows δ¹⁵N values decreasing with increasing altitude (Mannel et al. 2007). More studies should be conducted in other ecosystems with animals in a variety of trophic levels to expand our understanding of the effect of altitude on δ¹³C and δ¹⁵N of animals.

We discuss altitudinal patterns of feather δ¹³C and δ¹⁵N values of nine wild passerine species, belonging to three feeding guilds (Chen and Chou 1999, Lin et al. 2003) collected along a large altitudinal gradient of ~2,500 m in Taroko National Park, Taiwan (Fig. 1, Table 1):

Herbivores: Japanese White-eye (Zosterops japonicus), Taiwan Yuhina (Yuhina brumiceps); Omnivores: Grey-cheeked Fulvetta (Alcippe morrisonia), Steere’s Liocichla (Liocichla steerii), Grey-hooded Fulvetta (A. cinereiceps); and Insectivores: Collared Bush Robin (Tarsiger johnstoniae), Green-backed Tit (Parus monticolus), Rufous-capped Babbler (Stachyris ruficeps), White-browed Bush Robin (T. indicus).

Our first objective was to ascertain if δ¹³C values in feathers increased, while δ¹⁵N values in feathers decreased with increasing altitude for each guild and each species. Our second objective was to examine year-to-year and/or month-to-month fluctuations of δ¹³C and δ¹⁵N in feathers of birds. This would naturally reflect altitude and diet inferences. The presence or absence of
significantly different stable isotope values in feathers collected from the same bird but grown in different years would indicate if the bird exhibited year-to-year molting site fidelity. Similarly, fluctuations in stable isotope values between feathers grown at different times within a single year would indicate altitudinal movements of the bird during the period of feather growth. Third, we explored if nitrogen and carbon isotopes can be used as tracers to study altitudinal migration of montane birds in Taiwan. If feather nitrogen and carbon isotopic profiles are distinguishable among sites along an altitudinal gradient, these two isotopes would provide an opportunity to sample individuals at other times of the year to identify their origins.

METHODS

Study Sites.—We mist-netted birds at eight banding sites at different altitudes (100-3,000+ m) in Taiwan’s Taroko National Park (Fig. 1, Table 1) from July 2007 to January 2008. Taroko is in the northern section of the Central Mountain Range of Taiwan, and includes high mountains and steep gorges. Climate and vegetation changes, along with altitude, in this area create vegetation zones that can be generally classified as broadleaved forests (<1,500 m asl), mixed broadleaved and coniferous forests (between 1,500 and 3,000 m asl), and subalpine coniferous forests (>3,000 m asl) (Xu and Lin 1984). Most banding sites were in natural forests, but some areas within Sibao, Loshao, and Hehuan Farm have been used as vegetable plantations for many decades. The major vegetables cultivated on these farmlands are cabbages, peas, spinach, and tomatoes. The overall latitudinal and longitudinal spreads of these eight banding sites are less than 1°.

Feather Collections.—We collected feathers from each mist-netted bird for stable isotope analysis, but we also banded, classified as male or female (if possible), and recorded morphological and plumage characteristics for these birds prior to release. We collected the first primary feather from each wing of each bird mist-netted. Feathers which had a glossy color, no nicks in the outer webs, a visible terminal end of the rachis beyond the wing margin, and no abrasions were identified as new feathers grown in 2007. We assumed bleached and worn feathers were grown in 2006. We collected an old primary feather adjacent to the currently growing or newly grown feathers from each wing from those birds still in the process of molting, therefore having two generations of feathers. Some birds were captured more than once, and the feathers replacing the first primary feathers we had pulled previously were again sampled. We selected primary feathers because they are molted shortly after breeding and re-grown prior to migration in most passerines (Pyle et al. 1997), making them the most likely plumage to represent the isotopic values of molting locations.

All collected feathers were sealed in labeled, small paper envelopes and stored in a dry location prior to shipment to the United States for stable isotope analysis. All feathers were heated at 60°C for 30 min before shipping to meet the import requirements of the United States.

Feather Cleaning and Preparation.—We randomly selected one of the two collected feathers, including old feathers grown in 2006 and new feathers grown in 2007, from each band for analysis. Feathers were sonicated in distilled water for 30 min prior to isotopic analysis, followed by sonication in petroleum ether for an additional 30 min to remove contaminants from the feather surface. Feathers were then air-dried in a fume hood for 24 hrs. We cut sections weighing between 0.7 and 0.8 mg after feathers were cleaned and air-dried. We used most of the feather between the tip and the middle...
of the feather for $\delta^{13}$C and $\delta^{15}$N analysis because the feathers were small, wrapping each in a separate tin capsule. There is a concern regarding isotopic variations within a feather (Wassenaar and Hobson 2006, Chang et al. 2008), and we did not attempt to examine different portions within a feather because it was necessary to use a large portion of the feather.

**Isotopic Analysis.**—We analyzed $\delta^{13}$C and $\delta^{15}$N of the feather samples using an elemental analyzer (Costech ECS 4010, Valencia, CA, USA) coupled to a Delta V mass spectrometer (Finnigan, Bremen, Germany) at Brigham Young University. We used UCLA Carrera (a working standard from Ian Kaplan’s laboratory, UCLA, $\delta^{13}$C = 2.52‰) and LSVEC (NIST, $\delta^{13}$C = −46.5‰) as external standards for carbon, and USGS 25 (NIST, $\delta^{15}$N = −30.4‰) and USGS 26 (NIST, $\delta^{15}$N = 53.5‰) as external standards for nitrogen. Instrument precision for the measurements was ±0.2‰ for $\delta^{13}$C and $\delta^{15}$N.

All stable isotope ratios of the samples are reported in per mil (‰) using the “delta” ($\delta$) notation: $\delta_{\text{sample}} = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1,000$, where the $\delta_{\text{sample}}$ is the isotope ratio of the sample relative to the standard, and $R_{\text{sample}}$ and $R_{\text{standard}}$ are the fractions of heavy to light isotopes ($^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N) in the sample and standard, respectively. Delta values for carbon and nitrogen are expressed relative to PDB (Craig 1957) and atmospheric nitrogen (Mariotti 1983), respectively.

**Data Analysis.**—We limited our investigation of altitudinal trends and differences among sites for $\delta^{13}$C and $\delta^{15}$N values to first primary feathers grown in 2007 collected from birds at time of first capture. The relationships between values of $\delta^{13}$C, $\delta^{15}$N, and altitude for each guild and each species were analyzed using linear regression. Feather isotopic differences among sites for each guild and each species were measured using a one-way ANOVA for data with normal distribution (tested by Shapiro-Wilk normality test) or a Kruskal-Wallis test if data were not normally distributed. Tukey’s post hoc tests were used to identify differences in isotope values between sites for data with normal distribution, and Bonferroni’s post hoc tests were used to identify differences in isotope values between sites for data without normal distribution. Combined analysis of multiple isotopes should increase the power of site identification (Webster et al. 2002). We used both feather $\delta^{13}$C and $\delta^{15}$N values in a multivariate analysis of variance (MANOVA) with Wilks’ Lambda as the test statistic to identify feather isotopic differences among sites for each guild and each species. Bonferroni’s method was used to examine differences in isotope values between sites for post hoc tests of MANOVA. We used repeated-measure ANOVAs to examine year-to-year and within year fluctuations of feather $\delta^{13}$C and $\delta^{15}$N values sampled from the same individuals. We only used $\delta^{13}$C and $\delta^{15}$N values of the first primary feather collected the first time the bird was captured in 2007 compared to $\delta^{13}$C and $\delta^{15}$N values of an older primary feather collected from the same bird at the same time for year-to-year comparisons. We also examined the statistical power of non-significant results of the year-to-year and within year repeated-measure ANOVAs. All statistical analysis were calculated with SAS statistical software (SAS 2003).

**RESULTS**

**Altitudinal Pattern and Site Comparison of $\delta^{15}$N Values.**—Feather $\delta^{15}$N values exhibited varying relationships to altitude among guilds and among species (Figs. 2–4). Insectivores were the only group which had a significant decrease in feather $\delta^{15}$N values with increasing altitude (Fig. 4A). Feather $\delta^{15}$N values for other two guilds had no significant relationship to altitude (i.e., $P > 0.05$) (Figs. 2A and 3A). When analyzed by species, the Rufous-capped Babblers (Fig. 4D) was the only species which had significant decreases in feather $\delta^{15}$N values with increasing altitude (Fig. 4E). The $R^2$ of Rufous-capped Babbler and White-browed Bush Robins were 0.27 and 0.37, respectively. Feather $\delta^{15}$N values for the other seven species had no significant relationship to altitude (i.e., $P > 0.05$) (Figs. 2B, C; 3B, C; 4B, C).

Feather $\delta^{15}$N values were significantly different between some, but not all, sites for omnivores (Fig. 3A) and insectivores (Fig. 4A). Herbivores did not have significant differences across sites (Fig. 2A). When analyzed by species, feather $\delta^{15}$N values were significantly different between some, but not all, sites for Grey-cheeked Fulvetta (Fig. 3B), Grey-hooded Fulvetta (Fig. 3D), Rufous-capped Babbler (Fig. 4D), and White-browed Bush Robin (Fig. 4E). The other five species did not have significant differences across sites (Figs. 2B, C; 3C; 4B, C).
All species combined for herbivores

\[ \delta^{15}\text{N} = 0.14 \times \text{Alt} + 6.98 \quad (R^2 = 0.01, P = 0.78) \]

GLM; \( F_{6, 19} = 0.69, P = 0.66 \)

\[ \delta^{13}\text{C} = 0.66 \times \text{Alt} - 24.76 \quad (R^2 = 0.43, P < 0.001) \]

GLM; \( F_{6, 15} = 3.56, P = 0.016 \)

Japanese White-eye

\[ \delta^{15}\text{N} = -3.39 \times \text{Alt} + 9.84 \quad (R^2 = 0.30, P = 0.10) \]

Kruskal-Wallis test; \( H_2 = 3.68, P = 0.16 \)

\[ \delta^{13}\text{C} = 0.49 \times \text{Alt} - 24.60 \quad (R^2 = 0.15, P = 0.27) \]

Kruskal-Wallis test; \( H_2 = 2.46, P = 0.29 \)

Taiwan Yuhina

\[ \delta^{15}\text{N} = 1.36 \times \text{Alt} + 3.36 \quad (R^2 = 0.02, P = 0.62) \]

Kruskal-Wallis test; \( H_2 = 1.23, P = 0.75 \)

\[ \delta^{13}\text{C} = 1.29 \times \text{Alt} - 26.35 \quad (R^2 = 0.11, P = 0.20) \]

GLM; \( F_{5, 17} = 1.36, P = 0.30 \)

FIG. 2. Change in \( \delta^{15}\text{N} \) and \( \delta^{13}\text{C} \) values of feathers of herbivorous birds with altitude in Taroko National Park, Taiwan. Results of all species combined are shown in A and D. Results of individual species are shown in B, C, E and F. Stable isotope values of all individuals of each species collected at the same sites are expressed as means ± SE. Numbers of feathers used for isotope analyses for each species at different sites are in parentheses. Numbers of feathers used for isotope analyses for all species combined correspond to those of each species at different sites. One-way ANOVA results are also presented. Asterisks indicate significant differences \( (P < 0.05) \) between sites.

Altitudinal Pattern and Site Comparison in \( \delta^{13}\text{C} \) Values.—Feather \( \delta^{13}\text{C} \) values exhibited varying relationships to altitude among guilds and among species (Figs. 2–4). These values for both herbivores (Fig. 2D) and omnivores (Fig. 3E) decreased significantly with increasing altitude. Feather \( \delta^{13}\text{C} \) values for insectivores had no significant relationship to altitude (Fig. 4F). When analyzed by species, Grey-cheeked Fulvetas (Fig. 3F), Rufous-capped Babbler (Fig. 4I), and White-browed Bush Robins (Fig. 4J) had significant increases in feather \( \delta^{13}\text{C} \) values with increasing altitude. However, Grey-hooded Fulvetas (Fig. 3H) had significant decreases in feather \( \delta^{13}\text{C} \) values with increasing altitude. The \( R^2 \) of the four species varied between 0.14 and 0.35. The relationship for the other five species between feather \( \delta^{13}\text{C} \) values and altitude did not reach significance \( (P > 0.05) \) (Figs. 2E, F; 3G, H).

Feather \( \delta^{13}\text{C} \) values were significantly different between some, but not all, sites for all three guilds (Figs. 2D, 3E, 4F). When analyzed by species, \( \delta^{13}\text{C} \) values were significantly different between some, but not all, sites for Grey-cheeked Fulvetas (Fig. 3F), Steere’s Liocichla (Fig. 3G), Grey-hooded Fulvetas (Fig. 3H), Rufous-capped Babbler (Fig. 4I), and White-browed Bush Robins.
(Fig. 4J). The other four species had similar $\delta^{13}C$ values across sites (Figs. 2E, F; 4G, H).

**Combined Analysis of $\delta^{13}C$ and $\delta^{15}N$ Values Among Sites.**—MANOVA of $\delta^{13}C$ and $\delta^{15}N$ values of feathers from different sites revealed significant differences between some, but not all, sites for all three guilds (Figs. 5A, D; 6A; Appendices 1, 2). When analyzed by species, significant differences between some, but not all, sites were apparent for Grey-cheeked Fulvetas...
FIG. 4. Change in δ¹⁵N and δ¹³C values of feathers of insectivorous birds with altitude in Taroko National Park, Taiwan. Results of all species combined are shown in A and D. Results of individual species are shown in B, C, E and F. Stable isotope values of all individuals of each species collected at the same sites are expressed as means ± SE. Numbers of feathers used for isotope analyses for each species at different sites are in parentheses. Numbers of feathers used for isotope analyses for all species combined correspond to those of each species at different sites. One-way ANOVA results are also presented. Asterisks indicate significant differences (P < 0.05) between sites.
FIG. 5. MANOVA comparisons of sites for herbivorous and omnivorous birds. Results of all species combined are shown in A and D. Results of individual species are shown in B, C, and E–G. Stable isotope values of all individuals collected at the same sites are expressed as means ± SE. Numbers of feathers used for isotope analyses at different sites are in parentheses. Asterisks indicate significant differences (P < 0.05) between sites. Post hoc test results of D are in Appendix 1.
FIG. 6. MANOVA comparisons of sites of insectivorous birds. Results of all species combined are shown in A. Results of individual species are shown in B–E. Stable isotope values of all individuals collected at the same sites are expressed as means ± SE. Numbers of feathers used for isotope analyses at different sites are in parentheses. Asterisks indicate significant differences (P < 0.05) between sites. Results of post hoc test of A are in Appendix 2.

(Fig. 5E), Steere’s Liocichla (Fig. 5F), Grey-hooded Fulvettas (Fig. 5G), Rufous-capped Babblers (Fig. 6D), and White-browed Bush Robins (Fig. 6E). The other four species did not differ across sites (Figs. 5B, C; 6B, C).

Year-to-year and Within-year Comparisons.—Seven species had sufficient data for between-year (Fig. 7, Table 2) and six species for within-year (Fig. 7, Table 3) comparisons. Feathers for all species from the same individuals did not have significant between-year and within-year variations in δ¹³C. The power of the tests varied between 0.05 and 0.45. Feathers from the same individuals for δ¹⁵N values had no significant between-year and within-year variations in isotopic values for all species except Taiwan Yuhinas (F₁,₉ = 13.1, P = 0.006), and Steere’s Liocichlas (F₁,₁₃ = 4.9, P = 0.045). The δ¹⁵N values for
FIG. 7. \( \delta^{15}N \) and \( \delta^{13}C \) values of feathers grown in 2006 and 2007, as well as those grown at different times in 2007 but taken from the same individuals. The number in each square represents the number of the primary feather grown in 2006 used for isotope analyses, i.e., 7 in the square represents the seventh primary feather. Statistical results are in Tables 2 and 3. The code for each site corresponds to Fig. 1 and Table 1.
these two species in feathers grown in 2007 were significantly higher than those grown in 2006 (Fig. 7, Table 2). The power of these tests varied between 0.05 and 0.43.

**DISCUSSION**

**Altitudinal Trends in Feather $\delta^{13}N$ and $\delta^{13}C$ Values.**—A major finding was that there is no simple relationship between feather isotope values and altitude. Feather $\delta^{15}N$ values decreased significantly with increasing altitude for insectivores, but not for herbivores and omnivores. Feather $\delta^{13}C$ values increased significantly with increasing altitude for herbivores and omnivores, but not for insectivores. Altitudinal trends in feather $\delta^{15}N$ and $\delta^{13}C$ values exhibited more inconsistent patterns when analyzed by species; feather $\delta^{15}N$ and $\delta^{13}C$ values for some species increased significantly with increasing altitude, others decreased significantly with increasing altitude, and still others exhibited no significant relationship between isotopic values and altitude. In addition, these patterns do not reflect those typically reported for plants and soils (Mariotti et al. 1980; Korner et al. 1991), i.e., $\delta^{13}C$ values increasing (~1.1/°km) (Korner et al. 1991), and $\delta^{15}N$ values decreasing (~1.6/°km) (Mariotti et al. 1980; Handley et al. 1999; Jacot et al. 2000a, b; Schuur and Matson 2001; Amundson et al. 2003; Mannel et al. 2007) with increasing altitude.

The mechanisms responsible for altitudinal patterns in feather $\delta^{13}C$ and $\delta^{15}N$ values are still not understood, but the altitudinal patterns of feather $\delta^{13}C$ and $\delta^{15}N$ values could be interpreted by several interrelated hypotheses involving nutrition. First, $\delta^{13}C$ and $\delta^{15}N$ values of plants (Mariotti et al. 1980; Handley et al. 1999; Jacot et al. 2000a, b; Amundson et al. 2003; Mannel et al. 2007) and arthropods (Markow et al. 2000, Herrera et al. 2002, Hood-Nowotny and Knols 2007) exhibit interspecific differences. Previous studies conducted in Taroko show that plant (Xu and Lin 1984, Chen 1994) and insect (Xu 2006, 2007) species change with altitude. Assuming these birds stay locally at their molting sites, perhaps the lack of altitudinal patterns in feather $\delta^{13}C$ and $\delta^{15}N$ values in many of the species we
TABLE 2. Repeated-measures ANOVA for isotopic values of the feathers grown in 2006 and 2007 from the same individuals. Significant differences \((P < 0.05)\) are in bold italics. Degrees of freedom are indicated in parentheses \((df\) for numerator, \(df\) for denominator). Results \((1-\beta)\) of the power analysis are presented \((\alpha = 0.05)\). Sample sizes of each species are indicated in parentheses by the common name of each species.

<table>
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<tr>
<th>Species</th>
<th>(8^\text{15}N)</th>
<th>(P)</th>
<th>(1-\beta)</th>
<th>(8^\text{13}C)</th>
<th>(P)</th>
<th>(1-\beta)</th>
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<td>0.06</td>
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<td>0.07</td>
<td>0.00 (1, 13)</td>
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<td>Rufous-capped Babbler (12)</td>
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<td>0.43</td>
<td>0.37 (1, 11)</td>
<td>0.55</td>
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* Feathers grown in 2007 were significantly higher than those grown in 2006 (Fig. 7).

sampled may be attributed to individuals of these species consuming a variety of insects and/or plant matter during the time of molt which, when combined, cancel the effect of altitude. Similarly, increase/decrease of feather \(\delta^{13}C\) and \(\delta^{15}N\) values with increasing altitude for some species may also be due to the combination of foods they choose to eat, rather than to any effect of altitude. Detailed surveys of the isotopic ratios of foods and knowledge of diet-tissue fractionation \((Gannes et al. 1997)\) of these birds are both necessary for testing these hypotheses. Second, different individuals of the same species may move freely during feather growth between different resource patches along a wide range of altitudes to obtain their daily food requirements. Foraging over a wide altitudinal range may lead to feather \(\delta^{13}C\) and \(\delta^{15}N\) values that do not reflect expected altitudinal trends.

**Year-to-year and Within-year Comparison**—One can examine changes in diet or in feeding locations over time by repeatedly comparing isotopic values of tissue samples at different time intervals, but from the same source \((Dalerum and Angerbjorn 2005)\). Feathers are ideal for a temporal analysis of feeding locations \((Mizutani et al. 1990, Hobson and Clark 1992, Thompson and Furness 1995)\) because they can be collected continually from the same individual \((Ainley et al. 2003, Dalerum and Angerbjorn 2005)\). Our results show within-individual variation of feather \(\delta^{15}N\) and \(\delta^{13}C\) values is low both between- and

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<tr>
<th>Species</th>
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<tr>
<td>Collared Bush Robin (7)</td>
<td>4.44 (1, 5)</td>
<td>0.09</td>
<td>0.33</td>
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within-year for most of the species examined. This suggests these birds feed on similar diets and at similar feeding locations/altitudes when molting flight feathers both within a single season and from year to year. Also, these birds may exhibit strong feeding site fidelity during molt periods. However, the scale of what constitutes a feeding site as indicated by isotopic analysis of feathers is still unclear, and may not correspond to the exact locations where the birds were captured.

Taiwan Yuhinas and Steere’s Liocichlas had significant yearly variations in $\delta^{15}N$ values in this study. Thus, the differences in $\delta^{13}C$ values of the feathers of these species suggest that, from 1 year to the next, these birds either fed at different altitudes or remained at the same location but changed the composition of their diet, or remained at the same location and did not change the composition of their diet, but $\delta^{15}N$ values of the diet varied (Dalerum and Angerbjorn 2005).

Our attempt to separate individuals from different altitudes and to establish a sound isotope profile along the altitudinal gradient using feather carbon and nitrogen isotope was unsuccessful. Thus, these two isotopes do not appear to be suitable for the study of altitudinal migration of montane passerines in Taroko. First, we found either no significant differences between sites, or significant differences between some, but not all sites when investigating $\delta^{15}N$, and $\delta^{13}C$ separately or together regardless of whether the data are analyzed at the guild level or species level. Second, feathers reflect isotopic values at the time and location of molt (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 1998, Hobson 1999b, Wassenaar and Hobson 2000) and the application of stable isotopes to study bird migration relies on sound information of isotopic values across their altitudinal range. However, not only did we find instances where there were weak relationships between feather $\delta^{15}N$, $\delta^{13}C$, and altitude, but even where there was a significant relationship, the amount of variation explained by the relationships ($R^2$) was quite low. This is also the case in previous studies (Graves et al., 2002, Hobson et al. 2003, Mannel et al. 2007), although these studies suggested that $\delta^{15}N$ and $\delta^{13}C$ might be useful for studying the altitudinal movements of animals. While these studies found significant relationships between feather $\delta^{13}C$ or feather $\delta^{15}N$ and altitude, they did not indicate the $R^2$ value or discuss the predictive strength of the relationship. In contrast, our study suggests that carbon and nitrogen isotopes are not adequate to serve as regional markers of individuals or populations inhabiting different altitudes. While feather carbon and nitrogen isotopes exhibit a significant altitudinal trend for some guilds or species, it is not strongly predictive and does not appear to be useful for tracking altitudinal movement of montane passerines.

**ACKNOWLEDGMENTS**

We greatly appreciate B. V. Chu, Jian Hong Chen, Jia Hong Chen, and H. Y. Lin for help with fieldwork, and Talita Alencar, A. M. Johnson, and Jenilyn Weston for feather cleaning and sample preparation. We thank David Tingey for assistance with the isotope analysis. We are grateful to Ellen Paul for help and support with feather shipments. We thank Taroko National Park of Taiwan for financial and logistic support. This study was also supported by grants NSC 96-2621-B-024-001 from the National Science Council of Taiwan to HJS.

**LITERATURE CITED**


XU, Y. F. 2006. The community and function of insects in Taroko National Park (1). Taroko National Park, Hualien, Taiwan.


APPENDIX 1. Post hoc t-test of MANOVA for feather isotopic values (%) from sites of omnivorous birds. Asterisks and plus signs indicate significant ($P < 0.05$) and no ($P > 0.05$) differences between sites, respectively. The code for each site corresponds to Fig. 1 and Table 1.

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APPENDIX 2. Post hoc t-test of MANOVA for feather isotopic values (%) from sites of insectivorous birds. Asterisks and plus signs indicate significant ($P < 0.05$) and no ($P > 0.05$) differences between sites, respectively. The code for each site corresponds to Fig. 1 and Table 1.

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SEASONAL FECUNDITY AND SOURCE-SINK STATUS OF SHRUB-NESTING BIRDS IN A SOUTHWESTERN RIPARIAN CORRIDOR

L. ARRIANA BRAND1,3,4 AND BARRY R. NOON2

ABSTRACT.—Saltcedar (Tamarix spp.) has increasingly dominated riparian floodplains relative to native forests in the southwestern U.S., but little is known about its impacts on avian productivity or population status. We monitored 86 Arizona Bell’s Vireo (Vireo bellii arizonae), 147 Abert’s Towhee (Melozone aberti), and 154 Yellow-breasted Chat (Icteria virens) nests to assess reproductive parameters in cottonwood-willow (Populus-Salix), saltcedar, and mesquite (Prosopis spp.) stands along the San Pedro River, Arizona during 1999–2001. We also assessed source-sink status for each species in each vegetation type using field data combined with data from the literature. There were no significant differences in reproductive parameters between vegetation types for Abert’s Towhee or Yellow-breasted Chat, although seasonal fecundity was quite low across vegetation types for the latter (0.75 ± 0.14; mean ± SE). Bell’s Vireo had extremely low seasonal fecundity in saltcedar (0.10 ± 0.09) and significantly fewer fledglings per nest in saltcedar (0.09 ± 0.09) compared with cottonwood (1.07 ± 0.32). Point estimates of λ were substantially <1 for all three focal species in all habitats indicating the entire study area may be performing as a sink; 90% CI of λ included 1 only for Abert’s Towhee across vegetation types and Bell’s Vireo in cottonwood vegetation. These results are surprising given the San Pedro is considered to be one of the best remaining occurrences of lowland native riparian vegetation in the southwestern United States. Received 15 April 2010. Accepted 8 October 2010.

The proportion of lowland riparian corridors covered by exotic saltcedar (Tamarix spp.) relative to native broadleaf forests and shrublands has increased dramatically in the Southwest over the past 50 years (Hunter et al. 1987, Sher et al. 2000, Morisette et al. 2006, Stromberg et al. 2007). Avian density responses to these vegetation types have been documented in numerous studies across river systems, yet few studies have assessed measures of productivity for southwestern riparian birds. In particular, little is known about the impacts of exotic vegetation on avian productivity or population status in the region (Sogge et al. 2008).

Many canopy-nesting bird species have highest densities in tall, gallery cottonwood-willow (Populus-Salix) forests compared with saltcedar, although saltcedar has maintained high abundance of some shrub-nesting species (Hunter et al. 1987, 1988; Ellis 1995; Brand et al. 2008, 2010). Exotic vegetation is one circumstance in which patterns of abundance and productivity may diverge (Van Horne 1983, Battin 2004, Bock and Jones 2004); thus, it is important to assess productivity and population status for shrub-nesting birds in different habitat types comprised of native and exotic vegetation. Brand et al. (2010) documented nest survivorship of common shrub-nesting birds on the San Pedro River and found a tendency for Arizona Bell’s Vireo (Vireo bellii arizonae) to have higher nest survivorship in cottonwood versus mesquite (Prosopis spp.) and saltcedar, but no difference in nest survivorship between vegetation types for Yellow-breasted Chat (Icteria virens) and Abert’s Towhee (Melozone aberti). Nest survival is only one component of avian fecundity, and further work is needed to document productivity and population status for these species. Source-sink models have been applied extensively to assess habitat quality of fragmented versus contiguous habitats across the Midwest and other regions in the U.S. (e.g., Pulliam 1988, Donovan et al. 1995, Fauth 2000, Yackel Adams et al. 2007), but little is known about productivity or source-sink status of shrub-nesting birds in southwestern riparian habitats.

Our primary research objectives were to assess reproductive parameters (e.g., clutch size, young per nest, seasonal fecundity) and source-sink status of three relatively common shrub-nesting bird species on the San Pedro River in southeastern Arizona among vegetation types. This study supplements and provides greater context for previous nest survivorship estimates (Brand et al. 2010) for this population with additional
productivity measures and draws information from the literature to assess source-sink status. The San Pedro River is generally considered one of the best remaining examples of lowland riparian cottonwood-willow woodland and forests in the region. We hypothesized that native cottonwood-willow and mesquite riparian forests would maintain higher productivity and serve as population sources, and saltcedar would serve as a sink.

**METHODS**

We used estimates from field data collection supplemented with information from the literature to assess reproductive parameters and source-sink status for three shrub-nesting species with adequate data: Yellow-breasted Chat, Abert’s Towhee, and Arizona Bell’s Vireo. We collected field data at 23 sites on the San Pedro River during the 1999–2001 field seasons. Study sites included 16 areas within the San Pedro Riparian National Conservation Area (SPRNSCA) managed by the Bureau of Land Management (BLM) and seven sites on privately-owned land north of the SPRNCA (Fig. 1). Cottonwood-willow forests are the predominant woody vegetation type along the San Pedro River floodplain with saltcedar occurring in the drier stretches. A second zone of riparian vegetation occurs beyond the floodplain—river terraces on the San Pedro are vegetated mainly by mesquite forests.

We searched for and monitored nests in cottonwood, saltcedar, and mesquite stands every 2–5 days during the avian breeding season (10 May to 20 Jul) at each site following BBIRD protocol (Martin et al. 1997, Brand et al. 2010). We recorded egg or nestling age, adult behavior, and nest status at each nest check. Ages were based on observed laying dates, hatch dates, and nestling size and development. We estimated clutch size by counting the number of host eggs following onset of incubation. We considered nests failed if they showed clear signs of failure (e.g., torn or fallen nest, broken eggs, dead nestlings) or if the nest was intact but eggs or nestlings disappeared >2 days before the expected fledging date. We estimated the number of young fledged per nest by counting the number of nestlings observed within 2 days of the expected fledging date, and where there was direct observation of fledging or indirect evidence such as flattened nest rim and fecal material on the rim or below the nest.

The finite rate of population increase ($\lambda$) is a key parameter used to assess population status and, in particular, whether a population is functioning as a population source or sink (Pulliam 1988, Battin 2004). We used the finite rate of population increase ($\lambda$) in the absence of immigration or emigration to assess the status of each species within each vegetation type and across vegetation types. We calculated $\lambda = S_A + S_f \beta$ by vegetation type where $S_A$ is annual survival of adults, $S_f$ is annual survival of juveniles, and $\beta$ is seasonal fecundity, or the number of females produced per breeding female (Pulliam 1988). We estimated seasonal fecundity by vegetation type as $\beta = ns \cdot f \cdot a$, where $ns = \%$ nest survival by vegetation type, $f = \text{mean number of female young produced per successful nest by vegetation type}$, and $a = \text{average number of nesting attempts per season}$ (Pulliam 1988, Fauth 2000, Grzybowski and Pease 2005). We used estimates of $ns$ for each species in each vegetation type, and across all vegetation types, from a companion study of the same populations (Brand et al. 2010; Table 1).

That study used the method of Stanley (2000) to assess daily nest survival probability ($\hat{p}$) and then calculated nest survival as the percentage of clutches that resulted in ≥1 fledged offspring equal to $\hat{p}^{d_1} \cdot \hat{p}^{d_2} \cdot 100$, where $d_1$ and $d_2$ = average days in the incubation and nestling periods, respectively (Jehle et al. 2004). We estimated $f$ from field data as the total number of fledglings per successful nest divided by two, assuming an equal sex ratio at hatching. We considered species- and vegetation-specific estimates of nest survival and number of female young fledged per successful nest to represent 3-year breeding-season averages since nests were monitored throughout the breeding season and we combined data across years.

We did not measure the average number of nesting attempts by species per season on the San Pedro. Instead, we adopted estimates for each species from previous studies that followed all nesting attempts by a cohort of females though a breeding season. Based on previous studies, we assumed that Yellow-breasted Chat and Abert’s Towhee adult females nested 1.4 ± 0.1 (mean ± SE) and 3.9 ± 0.5 times on average per season, respectively (Thompson and Nolan 1973, Finch 1984). Budnik et al. (2001) reported average number of nesting attempts separately for parasitized versus non-parasitized pairs in recognition that birds parasitized by Brown-headed Cowbirds...
FIG. 1. San Pedro River showing bird sites, highways, cities, boundary between upper and lower basins, and San Pedro Riparian National Conservation Area (SPRNCA).
(Molothrus ater) may nest more frequently. We used average nesting attempts weighted by the proportion of nests parasitized by vegetation type from Brand et al. (2010) to account for this variation, and assumed that Bell’s Vireos nested 1.7 ± 0.2, 2.0 ± 0.1, 2.2 ± 0.2, and 2.0 ± 0.2 times (mean ± SE) in cottonwood, mesquite, saltcedar, and across all vegetation types, respectively (Budnik et al. 2001).

We used estimates of annual adult survival from the literature specific to the Southwest. The estimates were $S_A = 0.574 ± 0.072$ for Bell’s Vireo (mean ± SE), $S_A = 0.518 ± 0.028$ for Yellow-breasted Chat, and $S_A = 0.486 ± 0.126$ for Abert’s Towhee obtained from 6, 18, and 5 Monitoring of Avian Productivity and Survivorship (MAPS) stations in the southwestern U.S., respectively (DeSante and Kaschube 2006, Michel et al. 2006, Budnik et al. 2000). Juvenile survival estimates are lacking for these species, and we assumed that annual survival of juveniles was half that of adults (Temple and Carey 1988, Donovan et al. 1995, Budnik et al. 2000). Use of the same adult and juvenile survivorship estimates for the different vegetation types will tend to underestimate differences in $\lambda$ between them.

We estimated the standard error of $\beta$ and $\lambda$ using the delta method (Armstrong et al. 2002, Powell 2007). We assumed covariances = 0 since $S_A$, $n_s$, and $a$ were estimated with different data. Only one successful Bell’s Vireo nest was observed in saltcedar (thus SE = 0), and we substituted the estimated standard error of the number of fledglings per successful nest observed in mesquite (SE = 0.28) to represent maximum observed variability in the system for that species for the delta method estimation of SE($\beta$) and SE($\lambda$). We set $\alpha = 0.10$ to minimize the probability of a Type II error and interpreted meaningful differences in reproductive parameters among vegetation types in terms of non-overlapping 90% confidence intervals.

The population for $\lambda > 1$ was considered to be a potential source of emigrants and the population for $\lambda = 1$ was considered stable (Pulliam 1988). The population for $\lambda < 1$ was considered to demonstrate characteristics of a population sink (Pulliam 1988, Battin 2004). We set $\alpha = 0.10$ to minimize the probability of a Type II error and interpreted results with 90% confidence intervals (CI) around $\lambda$. We also separately estimated adult survivorship, seasonal fecundity, and the average number of nesting attempts required to obtain a stable population ($\lambda = 1$) with other vital rates held constant. We used this approach to assess whether estimated rates were within 90% confidence intervals of what was observed or assumed, and to provide insight into what survivorship levels would be needed to conceivably maintain a stable population on the San Pedro. We conducted a sensitivity analysis to assess what levels of parameters drawn from the literature—adult

### Table 1. Reproductive parameters (mean ± SE) for Abert’s Towhee, Yellow-breasted Chat, and Bell’s Vireo in saltcedar (SC), cottonwood (CW), mesquite (MQ), and across all vegetation types.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>$n$</th>
<th>% nest survival</th>
<th>Clutch size</th>
<th>Fledglings per nest</th>
<th>Fledglings per successful nest</th>
<th>Seasonal fecundity</th>
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</thead>
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<tr>
<td>Abert’s</td>
<td>SC</td>
<td>36</td>
<td>30 ± 9</td>
<td>2.80 ± 0.11</td>
<td>1.03 ± 0.22</td>
<td>2.13 ± 0.22</td>
<td>1.23 ± 0.43</td>
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<tr>
<td>Towhee</td>
<td>CW</td>
<td>45</td>
<td>29 ± 8</td>
<td>2.79 ± 0.09</td>
<td>1.19 ± 0.20</td>
<td>2.43 ± 0.13</td>
<td>1.32 ± 0.40</td>
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<td>MQ</td>
<td>66</td>
<td>30 ± 6</td>
<td>2.81 ± 0.09</td>
<td>1.07 ± 0.17</td>
<td>2.50 ± 0.15</td>
<td>1.43 ± 0.36</td>
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<td></td>
<td>ALL</td>
<td>147</td>
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<td>2.80 ± 0.05</td>
<td>1.09 ± 0.11</td>
<td>2.38 ± 0.09</td>
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<td>Yellow</td>
<td>SC</td>
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<td>30 ± 11</td>
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<tr>
<td>-breasted</td>
<td>CW</td>
<td>71</td>
<td>43 ± 7</td>
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<td>1.16 ± 0.20</td>
<td>2.64 ± 0.22</td>
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<tr>
<td>Chat</td>
<td>MQ</td>
<td>58</td>
<td>41 ± 7</td>
<td>3.56 ± 0.09</td>
<td>1.31 ± 0.21</td>
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<td>42 ± 4</td>
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<td>34 ± 13</td>
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<td>0.54 ± 0.11</td>
<td>2.14 ± 0.19</td>
<td>0.31 ± 0.09</td>
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</table>

- $n =$ total nest sample size.
- From Brand et al. 2010.
- Seasonal fecundity = mean number of female offspring (number of fledglings divided by 2) successfully fledged per adult female per year.
- $90\%$ CI = mean ± 1.645 x SE.
- SE = 0 as only one of 11 Bell’s Vireo nests found in saltcedar was successful.
survivorship and average number of nesting attempts—would be required to attain $\lambda = 1$ at observed levels of population-specific vital rates from the San Pedro—nest survival and number of young per successful nest—within each vegetation type.

RESULTS

We monitored 86, 147, and 154 Bell’s Vireo, Abert’s Towhee, and Yellow-breasted Chat nests, respectively, during a 72-day interval during the avian breeding season across 3 years. Clutch sizes were similar among vegetation types for all three species (Table 1). Estimated young per nest, young per successful nest, and seasonal fecundity were similar among vegetation types for Abert’s Towhee and Yellow-breasted Chat although seasonal fecundity estimates for Yellow-breasted Chat were quite low (Table 1). Bell’s Vireo had extremely low seasonal fecundity, particularly in saltcedar, and had significantly fewer fledglings per nest in saltcedar compared with cottonwood based on non-overlapping confidence intervals (Table 1).

Point estimates of $\lambda$ were substantially $< 1$ for Bell’s Vireo, Yellow-breasted Chat, and Abert’s Towhee in all vegetation types (Fig. 2). Bell’s Vireo had the greatest variation in $\lambda$ across vegetation types of the three species with 27 and 17% higher estimates in cottonwood compared with saltcedar and mesquite, respectively. The upper 90% confidence limit for $\lambda$ was $< 1$ for Bell’s Vireo and Yellow-breasted Chat in all habitat types with the exception of Bell’s Vireo in cottonwood where the upper confidence limit barely exceeded 1. CIs (90%) for Abert’s Towhee surrounding $\lambda$ were large and included 1 for all vegetation types.

Annual adult survivorship required to maintain $\lambda = 1$, at observed levels of seasonal fecundity, was 0.60 across vegetation types for Abert’s Towhee with little variation between vegetation types; estimates were within 90% CI of assumed survivorship (Fig. 3). Annual adult survivorship required to maintain $\lambda = 1$, at observed levels of seasonal fecundity, were 0.77, 0.72, 0.71, and 0.73 for Yellow-breasted Chat and 0.95, 0.87, 0.75, and 0.87 for Bell’s Vireo in saltcedar, mesquite, cottonwood, and across vegetation types, respectively; these estimates were higher than the upper 90% CI of assumed survivorship estimates.

Seasonal fecundity estimates needed to maintain a stable population ($\lambda = 1$), given assumed annual survivorship, were higher than observed for all species in all vegetation types and not within the 90% CIs of our estimates (Fig. 3). Seasonal fecundity needed for Bell’s Vireo to maintain a stable population was $\sim 15$, five, two, and five times higher than observed in saltcedar, mesquite, cottonwood, and across vegetation types, respectively. Seasonal fecundity to maintain a stable population needed to be about two and three times higher than observed across vegetation types for Abert’s Towhee and Yellow-breasted Chat (Fig. 3).

There was a strong trade-off between adult survivorship and average number of nesting
attempts needed to maintain a stable population in the absence of immigration at observed levels of nest productivity on the San Pedro (Fig. 4). Adult survivorship and/or the average number of nesting attempts required to maintain a stable population was high for Bell’s Vireo, and higher in mesquite and saltcedar than cottonwood, given observed nest survivorship and young per successful nest in the different vegetation types (Fig. 4). Levels of adult survivorship and average nesting attempts required to maintain a stable population were lower for Abert’s Towhee and Yellow-breasted Chat than Bell’s Vireo and varied little by vegetation type (Fig. 4).

**DISCUSSION**

Possible population sources (based on 90% CI of λ that included 1) only occurred for Abert’s Towhee across vegetation types and Bell’s Vireo in cottonwood vegetation using nest survival and productivity estimates from local populations and survivorship estimates from the literature. Our point estimates of λ were all substantially <1 indicating the entire study area may be operating as a population sink. These results are surprising given the San Pedro is considered to be one of the best remaining occurrences of lowland native riparian vegetation in North America (Noss et al. 1995).

We calculated annual survivorship required to maintain a stable population given observed fecundity levels to compare with what could conceivably occur. Annual survivorship required to maintain a stable population across vegetation types was within the 90% CI of our estimate for Abert’s Towhee (0.60), although we know of no...
Average number of nesting attempts

FIG. 4. Sensitivity analysis of different levels of adult survivorship by average number of nesting attempts at a stable population ($\lambda = 1$) when holding nest survivorship and number of female young per successful nest at observed levels from 23 sites along the San Pedro River 1999–2001 for Bell’s Vireo, Yellow-breasted Chat, and Abert’s Towhee in saltcedar (SC), cottonwood-willow (CW), mesquite (MQ), and across all vegetation types.

Other estimates from the literature. Estimated annual survivorship for Yellow-breasted Chat needed to maintain $\lambda = 1$ across vegetation types on the San Pedro (0.73) was higher than estimates from the Southeast (0.35 ± 0.04; mean ± SE) and Midwest (0.610 ± 0.067) (DeSante et al. 2001, DeSante and Kaschube 2006, Michel et al. 2006). Estimated annual survivorship for Bell’s Vireo needed to maintain $\lambda = 1$ across vegetation types (0.87) was well above estimates from the south-central region (0.56 ± 0.04; mean ± SE) and Midwest (0.61 ± 0.04) (Budnik et al. 2000, DeSante and Kaschube 2006, Michel et al. 2006); it was more similar to that of a long-lived raptor species such as California Condor (Gymnogyps californianus) (Meretsky et al. 1999). Estimates of annual survivorship required to maintain a stable population for Yellow-breasted Chat and Bell’s Vireo were higher than generally found for small passerine species (0.40–0.62; Martin 1995, DeSante and Kaschube 2006). Thus, at observed levels of fecundity and within the range of possible survivorship, it appears unlikely that Bell’s Vireo or Yellow-breasted Chat populations could maintain stable populations in the absence of immigration on the San Pedro over the study period.

Local estimates of adult and juvenile survivorship are needed to draw strong conclusions about population status. Population-specific estimates of adult and juvenile survivorship are lacking for the species we examined, and our results must be interpreted with caution. The estimates we used were drawn from the southwestern region (DeSante and Kaschube 2006, Michel et al. 2006), although we can only assume these estimates represent the specific location and vegetation types of interest. We used the common assumption of juvenile survivorship equal to half of adult survivorship. Data are lacking to assess the quality of this assumption, but the few studies that have directly estimated juvenile survivorship suggest this estimate may be slightly high and thus conservative (Gardali et al. 2003, Yackel Adams et al. 2007). The survival estimates we used were based on mark-recapture models that did not distinguish between mortality and emigration; they may underestimate true survivorship (McCoy et al. 1999). One approach that has been used is to add 0.1 to published estimates of adult survival to account for birds that dispersed (McCoy et al. 1999, Yackel Adams et al. 2007). When adult survivorship estimates are raised by 0.1, point estimates of $\lambda$ across vegetation types become 0.98 for Abert’s Towhee but still well below 1 (0.85 and 0.78) for Yellow-breasted Chat and Bell’s Vireo, respectively.

Observed fecundity was low on the San Pedro, particularly for Yellow-breasted Chat and Bell’s Vireo. High nest-predation rates can profoundly decrease nest survival. Nest-predation rates for Bell’s Vireo on the San Pedro varied by vegetation type with 55, 51, and 33% of nests preyed upon in saltcedar, mesquite, and cottonwood, respectively (Brand et al. 2010). These nest-predation rates were generally higher than those on the Bill Williams River (16–31%; Averill-Murray et al. 1999). Nest-predation rates
were also quite high for Yellow-breasted Chat (37–46%) and Abert’s Towhee (43–50%) on the San Pedro across vegetation types (Brand et al. 2010).

Nest parasitism by Brown-headed Cowbirds can reduce both nest survival and young fledged per successful nest. Nest survival rates observed for Bell’s Vireos on the San Pedro were low, particularly in saltcedar and mesquite, and similar to those recorded along the Bill Williams River (Averill-Murray et al. 1999). Parasitism rate decreased on the Bill Williams River and Bell’s Vireo nest survival increased by over 400% in the breeding season following initiation of cowbird control and cessation of adjacent ranching operations (Averill-Murray et al. 1999). Cowbird parasitism rates for Arizona Bell’s Vireos on the San Pedro were substantially higher in saltcedar (73%) and mesquite (60%) compared with cottonwood (33%; Brand et al. 2010). These rates in saltcedar and mesquite were lower than those observed on the Bill Williams River, but higher than most of those observed for federally listed Least Bell’s Vireo (Vireo bellii pusillus) and Southwestern Willow Flycatcher (Empidonax traillii extimus) across the region (Averill-Murray et al. 1999, Finch and Stoleson 2000, Kus and Whitfield 2005, Kus et al. 2010). In contrast, Abert’s Towhee parasitism rates were low on the San Pedro across vegetation types (11–17%) compared with those on the Lower Colorado River (Finch 1983, Brand et al. 2010). There were also substantially fewer fledglings for parasitized versus unparasitized nests on the Lower Colorado (Finch 1983). Parasitism rates were intermediate for Yellow-breasted Chat on the San Pedro (42, 41, and 23% in saltcedar, mesquite, and cottonwood, respectively; Brand et al. 2010). In comparison, no chat nests were parasitized by Brown-headed Cowbirds in a study in central Kentucky (Ricketts and Ritchison 2000).

The average number of nesting attempts per breeding season has a strong effect on annual fecundity (Schmidt and Whelan 1999, Grzybow-ski and Pease 2005). This parameter is difficult to measure because it requires birds to be color banded and followed throughout a breeding season. Renesting can be influenced by cowbird parasitism and we were able to incorporate different average nesting attempts by vegetation type for Bell’s Vireo (Budnik et al. 2001). Our estimate of the average number of nesting attempts for Abert’s Towhee came from a population with about twice the rate of parasitism compared with the San Pedro (Finch 1984, Brand et al. 2010); thus, the estimate may have been high for the San Pedro population. Of the three species, average number of nesting attempts was most likely underestimated for Yellow-breasted Chat, since estimated nesting attempts came from a population with apparently lower parasitism rates (Thompson and Nolan 1973).

The average number of nesting attempts per season required to maintain a stable population based on our sensitivity analysis was 6.0 for Abert’s Towhee and 3.5 for Yellow-breasted Chat with little variation between vegetation types. Abert’s Towhee is a resident species with a long nesting season, but an average of six attempts per season is beyond the 90% CI of what was observed for 10 pairs; only two (20%) females attempted to nest > five times in a season (Finch 1984). The Yellow-breasted Chat is a neotropical migrant with a much shorter nesting season, and 3.5 nests per season is beyond the 90% CI of what was observed for 24 pairs; only two (8%) females attempted to nest > two times in a season (Thompson and Nolan 1973). We estimated that 10 average nesting attempts per season would be required for a stable Bell’s Vireo population on the San Pedro across all vegetation types (33, 11, and 4 in saltcedar, mesquite, and cottonwood, respectively) when holding other vital rates at assumed or observed levels, Kus et al. (2010) reported a maximum of seven nesting attempts for individual Bell’s Vireos across all studies with population averages similar to those used in this study; ≥ 10 average nesting attempts per season to maintain a stable population in all vegetation types except cottonwood would almost certainly be beyond the physiological capabilities of Bell’s Vireos.

Year-to-year variation in fecundity rates can be substantial for some species (Eckerle and Thompson 2001) and it is important to evaluate if our fecundity estimates are representative. Average annual precipitation can strongly influence bird populations in semi-arid regions. For example, Abert’s Towhee density and productivity decreased in years with lower precipitation (Marshall 1960, Meents et al. 1981). The years of data collection in this study occurred over one of three major statewide droughts during the 20th century (Jacobs et al. 2005) and the subsequent 7 years of combined precipitation (2003–2010) in southeastern Arizona averaged 85% of normal (1971–
levels (U.S. Department of Commerce 2010). Our estimates likely represent drought conditions that have continued to be representative and may endure with projected climatic conditions (Dixon et al. 2009).

We are not aware of other source-sink or population status results from the region to compare for these species. Yellow-breasted Chat and Abert’s Towhee had stable trends in Arizona over the last 10- and 40-year periods based on Breeding Bird Survey (BBS) data (Sauer et al. 2007). However, BBS population trends for these species were highly variable in Arizona over the period of the study (Sauer et al. 2007), which may indicate variability in population status among riparian systems. Further documentation of population status, habitat selection, and habitat quality among watersheds over a similar time period is needed to gain landscape and regional perspectives of population dynamics for these species. Bell’s Vireos in Arizona, also based on Breeding Bird Survey (BBS) trends, had a non-significant decline over the past 40-years (−2.3% per year, \( P = 0.38 \)) but declined significantly over the past 10-years (−3.7% per year, \( P = 0.0001; \) Sauer et al. 2007). The low nest survival rates on the Bill Williams River (Averill-Murray et al. 1999) and low seasonal fecundity and \( \lambda \) estimates in this study for the San Pedro are surprising since these rivers should represent some of the best habitat within the limited range of Arizona Bell’s Vireos (Kus et al. 2010). There is increasing evidence that additional conservation focus is needed for Bell’s Vireos in Arizona. The status of these species depends on their fecundity and survivorship, and we believe the future research effort needed to obtain this information from local populations is warranted.

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**LITERATURE CITED**


Donovan, T. M., F. R. Thompson III, J. Faaborg, and J.


Stromberg, J. C., S. J. Litt, R. Marler, C. Paradzick, P.


ABSTRACT.—Herbaceous buffers are strips of herbaceous vegetation planted between working agricultural land and streams or wetlands. Mowing is a common maintenance practice to control woody plants and noxious weeds in herbaceous buffers. Buffers enrolled in Maryland’s Conservation Reserve Enhancement Program (CREP) cannot be mowed during the primary bird nesting season between 15 April and 15 August. Most mowing of buffers in Maryland occurs in late summer or fall, leaving the vegetation short until the following spring. We studied the response of wintering birds to fall mowing of buffers. We mowed one section to 10–15 cm in 13 buffers and kept another section unmowed. Ninety-two percent of birds detected in buffers were grassland or scrub-shrub species, and 98% of all birds detected were in unmowed buffers. Total bird abundance, species richness, and total avian conservation value were significantly greater in unmowed buffers, and Savannah Sparrows (*Passerculus sandwichensis*), Song Sparrows (*Melospiza melodia*), and White-throated Sparrows (*Zonotrichia albicollis*) were significantly more abundant in unmowed buffers. Wintering bird use of mowed buffers was less than in unmowed buffers. Leaving herbaceous buffers unmowed through winter will likely provide better habitat for wintering birds. Received 21 December 2009. Accepted 23 August 2010.

Herbaceous buffers are strips of herbaceous vegetation planted between working agricultural land and streams or wetlands. They are designed to manage environmental concerns such as water quality and can provide habitat for a variety of wildlife species (Clark and Reeder 2005). The U.S. Department of Agriculture’s (USDA) Conservation Reserve Program (CRP) offers several types of herbaceous buffer practices to agricultural producers, and Maryland’s Conservation Reserve Enhancement Program (CREP) offers additional financial incentives for landowner enrollment. Over 15,000 ha of herbaceous buffers are established in Maryland through the CRP (USDA 2010), most of which are enrolled in Maryland’s CREP. Herbaceous buffers in Maryland are usually planted either to native warm-season grasses or cool-season grasses with the addition of native wildflowers or introduced legumes (USDA 2009b).

Maintenance is required to keep CREP plantings in Maryland in good condition and functioning properly (USDA 2009b). Mowing is a common maintenance practice to control woody plants and noxious weeds in herbaceous plantings. Mowing is generally not allowed on CRP or CREP land during the primary nesting and brood rearing seasons for wildlife (dates vary from state to state), but is allowed during the rest of the year. Maryland’s CREP land may not be mowed between 15 April and 15 August (USDA 2009b). Most mowing of buffers in Maryland occurs in late summer or fall (hereafter, fall mowing) and often within a few days of 15 August (P. V. Barry, pers. comm.; J. E. Gerber, pers. comm.). Fall mowing is also a common practice in herbaceous CRP plantings in other states, including Virginia (G. I. Hall, pers. comm.), Ohio (M. D. DeBrock, pers. comm.), and Tennessee (M. E. Zeman, pers. comm.). Fall mowing leaves the vegetation short until growth begins the following spring. Farm managers often choose to mow in fall instead of late winter or spring because they believe shorter grass looks better, the ground may be too wet in spring for mowing, or fall is when they have the most time available (S. V. Strano, pers. comm.).

It is recommended that buffers be mowed no more than once every 2 to 3 years with no more than half of the area mowed in any 1 year (USDA 2009b). A common recommendation is to mow a third of each buffer every year on a 3-year rotation (USDA 2009b). However, some farm managers mow entire buffers each year (PJB, pers. obs.). Buffers often represent the only uncultivated herbaceous areas on farmland in Maryland and may be important habitat for early-successional birds. Many studies have evaluated the response by breeding birds to mowing of early-successional
habitats (e.g., Swanson et al. 1999, Warren and Anderson 2005, Zuckerberg and Vickery 2006), but few studies have evaluated the effects of mowing on wintering bird communities. We studied the response of wintering birds to fall mowing of herbaceous buffers. We hypothesized that wintering bird abundances, species richness, and total avian conservation value would be less in mowed than in unmowed buffers. We focus on the response of grassland and scrub-shrub birds because they are experiencing substantial population declines (Sauer et al. 2008) and are of high conservation concern (Hunter et al. 2001, Askins et al. 2007).

**METHODS**

**Study Area.**—The Eastern Shore of Maryland (east of Chesapeake Bay) has ~46% of landcover in farms (USDA 2009a) and 77% of the CREP buffers in the state (USDA 2007). Filter strips (USDA Practice CP21) are the most common type of herbaceous buffers in Maryland (USDA 2010). We conducted an experiment in 13 filter strips (hereafter, buffers) among two counties (Queen Anne’s and Talbot) on Maryland’s Eastern Shore.

All buffers selected were installed between 1997 and 2004, and were ≥3 years of age at the time of the study. Each buffer was between a rowcrop field and a forested wetland, which is a common location of buffers in Maryland. The adjacent rowcrops had been planted to either corn or soybeans in the previous growing season, and most were planted to winter wheat after fall harvest.

Nine buffers were planted with cool-season grasses and four were planted with warm-season grasses. Common warm-season grasses were big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and broomsedge bluestem (*A. virginicus*). The most common cool-season grass in buffers was orchardgrass (*Dactylis glomerata*), but other cool-season grasses including red (*Festuca rubra*) and sheep (*F. ovina*) fescue were also planted.

We established two treatments in each buffer: (1) a section (experimental treatment) mowed in late summer or fall (Aug–Dec) to 10-15 cm in height, and (2) an unmowed section. Mowed and unmowed treatments were randomly located along the length of the buffer and spanned the entire width of the buffer. We established one study site in each treatment. Each study site spanned the width of the buffer, was ≥50 m from the ends of the buffer and from the interface with the other treatment, and ≥100 m from the other study site in the same buffer. Mowed and unmowed study sites among all buffers were similar (X ± SD) in length (mowed: 176.0 ± 50.0 m; unmowed: 176.6 ± 50.3 m).

We defined the width of each buffer as the distance from the crop edge to the wooded edge and calculated width by averaging measurements taken every 50 m over the length of the buffer. Buffers ranged in width from 11 to 91 m, and average buffer width was 40.9 ± 35.7 m. We measured the length of each study site in a Geographic Information System (GIS) and calculated the area of each site by multiplying site width by site length.

**Vegetation Surveys.**—We conducted vegetation surveys once at each study site in winter 2007. We established one transect line through the center of the site in buffers <45 m wide, and two transect lines spaced evenly across the width of the site in buffers >45 m wide. We measured vegetation structure characteristics within 1-m² sampling plots at random distances perpendicular to five points spaced evenly apart along each transect line. Thus, we surveyed vegetation at five plots in buffers <45 m wide and 10 plots in buffers >45 m wide. We visually estimated the percent cover (non-overlapping) of grasses, forbs, trees, bare ground, and litter in each plot. We also measured vertical vegetation density (Robel et al. 1970), litter depth, and maximum vegetation height.

**Bird Surveys.**—We conducted three bird surveys at each study site between 19 January and 10 March 2007. All surveys were between 1 hr after sunrise and 1 hr before sunset. We did not conduct surveys in precipitation, fog, or wind >16 km/hr. Bird surveys in the two study sites in the same buffer were subsequent to one another and in random order. Individual birds observed in one study site were not observed to move to any other study sites, and study sites were considered independent.

We surveyed birds across the entire area of each study site. All surveys were conducted simultaneously by P. J. Blank and J. R. Parks. We walked parallel to the wooded edge of the buffer ≤20 m apart. The distance between us varied depending on width of the buffer. Nine buffers were ≤40 m wide and required only one pass. Four buffers were >80 m wide and required...
three passes. We communicated regularly and watched for birds moving within study sites so that individual birds were not counted twice. By using these methods, at least one observer walked within 10 m of all points in the study sites. Diefenbach et al. (2003) reported nearly 100% detection of breeding grassland birds within 25 m of observers, and Roberts and Schnell (2006) recommended that observers walk within 10 m of all points in fixed areas when calculating density of wintering grassland birds. Thus, we assumed 100% detection during our surveys. One observation of an American Kestrel (Falco sparverius) observed foraging above a study site during a survey was included in the counts.

**Statistical Analyses.**—We used three bird community metrics to compare bird use of mowed and unmowed buffers: total abundance, species richness, and total avian conservation value (TACV). The latter is an index used to assess the relative conservation value of different sites that incorporates the biological vulnerability and the regional importance of each species (Nuttle et al. 2003). We calculated TACV by multiplying each species’ abundance by its Partners in Flight conservation priority rank (Carter et al. 2000, Blank et al. 2011). We only analyzed the species-specific responses of Savannah Sparrow (Passerculus sandwichensis), Song Sparrow (Melospiza melodia), and White-throated Sparrow (Zonotrichia albicollis) because we could not fit appropriate models to the distribution of other species due to a lack of detections in most study sites. We considered a test result statistically significant at $P = 0.05$.

**RESULTS**

Vertical vegetation density, maximum height, percent cover of grass, and percent cover of forbs were significantly greater in unmowed than in mowed buffers (Table 1). We detected 412 birds in buffers, of which 98% were in unmowed buffers. We observed five species in mowed buffers and 14 species in unmowed buffers. Eight species were grassland or scrub-shrub birds (Table 2) and constituted 92% of all detections. The Song Sparrow was the most abundant species (45% of detections), followed by Field Sparrow (Spizella pusilla; 19%), and Savannah Sparrow (10%). Savannah Sparrow ($F_{1,12} = 6.36, P = 0.027$), Song Sparrow ($F_{1,12} = 16.54, P = 0.001$), and White-throated Sparrow ($F_{1,12} = 5.68, P = 0.035$) were all more abundant in unmowed than in mowed buffers. Total abundance, species richness, and TACV were all greater in unmowed than in mowed buffers (Table 3).

**DISCUSSION**

Wintering bird use of mowed buffers was less than in unmowed buffers. All bird community included width as a covariate because buffer width influences bird communities (Best 2000, Clark and Reeder 2005, Blank et al. 2011).

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**TABLE 1.** Vegetation characteristics (mean ± SE) in mowed and unmowed buffers on the Eastern Shore of Maryland, winter 2007.

<table>
<thead>
<tr>
<th>Vegetation characteristic</th>
<th>Management type</th>
<th>Mowed</th>
<th>Unmowed</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical density, cm</td>
<td></td>
<td>5.5 ± 0.9</td>
<td>21.9 ± 2.7</td>
<td>115.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Maximum height, cm</td>
<td></td>
<td>3.2 ± 0.1</td>
<td>4.6 ± 0.1</td>
<td>158.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Litter depth, cm</td>
<td></td>
<td>4.7 ± 0.7</td>
<td>4.4 ± 0.7</td>
<td>0.1</td>
<td>0.72</td>
</tr>
<tr>
<td>Percent cover</td>
<td></td>
<td>3.2 ± 0.2</td>
<td>3.6 ± 0.2</td>
<td>5.1</td>
<td>0.045</td>
</tr>
<tr>
<td>Grass</td>
<td></td>
<td>4.1 ± 2.1</td>
<td>5.7 ± 3.0</td>
<td>8.2</td>
<td>0.016</td>
</tr>
<tr>
<td>Forbs</td>
<td></td>
<td>0.1 ± 0.1</td>
<td>0.6 ± 0.3</td>
<td>4.0</td>
<td>0.070</td>
</tr>
<tr>
<td>Trees</td>
<td></td>
<td>3.9 ± 0.4</td>
<td>3.5 ± 0.4</td>
<td>3.7</td>
<td>0.078</td>
</tr>
<tr>
<td>Litter</td>
<td></td>
<td>5.1 ± 1.4</td>
<td>2.9 ± 2.6</td>
<td>3.5</td>
<td>0.086</td>
</tr>
<tr>
<td>Bare ground</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
metrics and species' abundances tested were significantly greater in unmowed than in mowed buffers, and 98% of all bird detections were in unmowed buffers. Wintering birds use herbaceous habitats for foraging, roosting, and escape cover (Watts 1990, Marcus et al. 2000, Smith et al. 2005, Conover et al. 2007) and fall mowing removes valuable habitat that wintering birds could otherwise exploit (Harper 2007).

These results are especially important because most birds detected in unmowed buffers were grassland or scrub-shrub species, two guilds experiencing substantial population declines (Hunter et al. 2001, Askins et al. 2007, Sauer et al. 2008). Three species detected in buffers (Field Sparrow, Savannah Sparrow, and Dark-eyed Junco [Junco hyemalis]) are listed as species of greatest conservation need in Maryland (Maryland Department of Natural Resources 2004). Thus, reducing the practice of fall mowing could provide additional habitat for several birds of conservation concern.

Our findings agree with other studies of wintering bird use in mowed and unmowed herbaceous habitats. Saab and Petit (1992) reported relative bird abundance and species richness were lower on grazed pastures maintained by mowing compared to abandoned pastures in Belize. Marcus et al. (2000) found greater sparrow abundance in herbaceous field borders than in mowed field edges in North Carolina. However, compared to studies of breeding birds, there have been few studies on the response of wintering birds to mowing of herbaceous habitats.

This study focused on the response of wintering birds to fall mowing but did not examine bird response to mowing at other times of year. Late winter or early spring mowing instead of fall mowing could provide additional habitat for wintering birds (Harper 2007). For example, mowing a buffer on 15 March instead of 15 August could provide 7 months of additional unmowed habitat. There are practical reasons why fall mowing may be preferred, including wet weather or lack of time to mow in late winter or early spring, that should be considered prior to altering mowing schedules. Late winter or early spring mowing may also remove habitat for wintering birds that may have become dependent on unmowed buffers for food or cover. When mowing is necessary, leaving nearby herbaceous areas unmowed will provide habitat that may be a refuge for some bird species (Bryan and Best 1991). Following the recommended guideline of mowing one-third of the area per year will provide more habitat for wintering birds than completely mowing buffers.

### TABLE 2. Mean density (birds/10 ha ± SD) of grassland and scrub-shrub bird species detected in mowed and unmowed buffers on the Eastern Shore of Maryland, winter 2007.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Mowed</th>
<th>Unmowed</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Kestrel</td>
<td>Falco sparverius</td>
<td>0.0 ± 0.0</td>
<td>0.1 ± 0.5</td>
</tr>
<tr>
<td>Eastern Bluebird</td>
<td>Sialia sialis</td>
<td>0.0 ± 0.0</td>
<td>0.1 ± 0.4</td>
</tr>
<tr>
<td>Field Sparrow</td>
<td>Spizella pusilla</td>
<td>0.0 ± 0.0</td>
<td>11.3 ± 34.7</td>
</tr>
<tr>
<td>Savannah Sparrow</td>
<td>Passerculus sandwichensis</td>
<td>0.6 ± 2.1</td>
<td>7.2 ± 16.2</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>Melospiza melodia</td>
<td>2.1 ± 5.3</td>
<td>70.1 ± 60.1</td>
</tr>
<tr>
<td>Swamp Sparrow</td>
<td>M. georgiana</td>
<td>0.0 ± 0.0</td>
<td>5.5 ± 13.3</td>
</tr>
<tr>
<td>White-throated Sparrow</td>
<td>Zonotrichia albicollis</td>
<td>1.6 ± 5.7</td>
<td>15.9 ± 51.0</td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>Junco hyemalis</td>
<td>0.7 ± 2.4</td>
<td>3.4 ± 12.2</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Bird community metric</th>
<th>Mowed</th>
<th>Unmowed</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total abundance</td>
<td>0.3 ± 0.2</td>
<td>11.0 ± 3.1</td>
<td>48.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species richness</td>
<td>0.5 ± 0.3</td>
<td>3.3 ± 0.8</td>
<td>11.0</td>
<td>0.006</td>
</tr>
<tr>
<td>Total avian conservation value</td>
<td>0.4 ± 0.2</td>
<td>19.9 ± 5.8</td>
<td>94.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Mowing should not be the sole form of management in herbaceous plantings to maintain early successional habitat (McCoy et al. 2001, Harper 2007). Mowing can accelerate grass succession and litter accumulation which creates unfavorable conditions for wildlife (McCoy et al. 2001). Burning, discing, and targeted herbicide applications may be more effective than mowing for maintaining optimal early successional habitat for wildlife (Harper 2007).

CONSERVATION IMPLICATIONS

Our results clearly indicate the negative impacts of fall mowing of herbaceous buffers on wintering bird communities in Maryland. This study has implications for the mowing schedules of many types of herbaceous habitats, including lawns, meadows, grasslands, and powerline rights-of-ways, and has particular relevance to management of herbaceous CRP or CREP plantings. When possible, leaving these herbaceous areas unmowed through winter will likely provide better habitat for wintering birds.

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INTERSPECIFIC VARIATION IN HABITAT PREFERENCES OF GRASSLAND BIRDS WINTERING IN SOUTHERN PINE SAVANNAS

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ABSTRACT.—We studied wintering grassland bird communities in De Soto National Forest in southern Mississippi, USA to assess differences in bird communities and vegetation structure among different stand types. We also examined which vegetation structure and plant species predicted occurrence of Bachman’s Sparrow (Peucaea aestivalis), Henslow’s Sparrow (Ammodramus henslowii), and Sedge Wren (Cistothorus platensis). Bachman’s Sparrows occurred only in uplands (x = 0.5 birds/ha) and stands managed for Red-cockaded Woodpeckers (Picoides borealis; x = 0.9 birds/ha), Henslow’s Sparrows occurred only in bogs (x = 3.8 birds/ha) and stands managed for Red-cockaded Woodpeckers (x = 2.1 birds/ha), while Sedge Wrens occurred in all stand types (x = 0.1–0.3 birds/ha). There were no significant differences among stand types in total bird densities for all three species combined. Dense, spatially uniform herbaceous cover and cover of Scleria muhlenbergii, a preferred food item in bogs, best predicted Henslow’s Sparrow occurrence (39% $r^2$ explained). Increased woody understory vegetation and decreased tree density best predicted Sedge Wren occurrence (17% $r^2$ explained). Management for Henslow’s Sparrows should focus on small-scale herbaceous ground-layer restoration in bogs. Bachman’s Sparrows will respond more to thinning dense upland stands. Sedge Wrens and Bachman’s Sparrows benefit from Red-cockaded Woodpecker management, whereas Henslow’s Sparrow use of woodpecker stands is ephemeral. Received 6 March 2010. Accepted 9 September 2010.

Virtually all remaining longleaf pine (Pinus palustris) savannas are subject to management for habitat improvement and sensitive species. Management, such as that for Red-cockaded Woodpeckers (Picoides borealis; hereafter RCW), may alter portions of forest stands in ways that create distinct patches. Natural variation in local topography in pine savannas, combined with forest management, leads to a variety of localized habitat types that differ in plant species composition and structure (Kirkman et al. 2001, Drewa et al. 2002a). These differences may also be reflected in grassland bird habitat preferences. Understanding these preferences is crucial for developing efficient species-specific conservation plans.

The majority of pine savanna habitats in De Soto National Forest (DSNF) can be divided into three distinct types: (1) upland pine stands (“uplands”), (2) upland pine stands managed for RCWs (“RCW”), and (3) hillside seepage pitcher plant (Sarracenia spp.) bogs (“bogs”). RCW clusters are an artificially designated stand type, whereas uplands and bogs are naturally occurring and well documented in the literature (Clewell 1986, Olson and Platt 1995).

Concern over the impact of ecosystem management on non-target species has sparked interest in the effects of RCW management on other organisms (Hunter et al. 1994, Brennan et al. 1995, Provencher et al. 2002). Several studies have shown stands managed for RCWs contain different bird communities than unmanaged stands and have higher densities of Bachman’s Sparrows (Peucaea aestivalis) (Conner et al. 2002, Provencher et al. 2002, Wood et al. 2004). No published studies have documented RCW cluster use by Henslow’s Sparrow (Ammodramus henslowii) or Sedge Wren (Cistothorus platensis), common wintering grassland birds in pine savannas.

Few studies have examined grassland bird preferences among habitat types in pine savannas. Some studies suggest Henslow’s Sparrows may prefer bogs over uplands (Plentovich et al. 1999, Tucker and Robinson 2003), while others have found birds in upland stands (Carrie et al. 2002, Johnson 2006, Palasz et al. 2010). Henslow’s Sparrows generally use both upland longleaf pine savannas and bogs, but may prefer bogs when both habitat types are in close proximity. Bachman’s Sparrow habitat preferences across different stand types have rarely been studied in winter. Allen et al. (2006) found breeding Bachman’s Sparrows were more common in upland habitats compared to wetter pocosins, a type of bog, in North Carolina longleaf pine savannas. Bachman’s Sparrows, as is also the case for Henslow’s Sparrows (Bechtoldt and Stouffer 2005), prefer to winter in grasslands that were burned in the previous growing season (Cox and Jones 2009).
Our focal species were three wintering grassland birds that frequent pine savannas along the Gulf Coast: Bachman’s Sparrow, Henslow’s Sparrow, and Sedge Wren. Numerous studies over the last decade have examined wintering Henslow’s Sparrow ecology, but few have reported habitat preferences among a mosaic of localized habitat types. Bachman’s Sparrow and Sedge Wren rarely have been studied in winter, and most reports of Bachman’s Sparrows using RCW clusters are from the breeding season. We do not know of published studies on Sedge Wren habitat preferences in southern pine savannas (Herkert et al. 2001). Our objectives were to: (1) assess differences in wintering grassland bird communities and vegetation structure among upland, RCW, and bog stands, and (2) ascertain which vegetation structures and plant species predict occurrence within a stand by Henslow’s Sparrows and Sedge Wrens.

METHODS

Study Area.—De Soto National Forest (153,780 ha) in southern Mississippi, USA is mostly managed for longleaf and slash pine (Pinus elliottii). The majority of pine savanna habitats in DSNF are upland stands, and many of these areas have severe shrub (Ilex spp., Gaylussacia spp.) encroachment due to past fire suppression (Brooks 2010). The pine savanna ecotypes in DSNF are described as xeric sand barrens and uplands, subxeric sandy uplands, and seeps (Peet 2006).

We selected 27 study sites to sample grassland birds. Ten sites were classified as upland stands, 10 as bog stands, six were managed RCW clusters, and one was classified as other. Our selection criteria were that each site needed >50% herbaceous cover and <50% shrub cover. Sites with >50% shrub cover were considered a priori to be unsuitable for grassland birds. We established 100-400 m of 20-m wide transects in upland, bog, and RCW clusters. These plots were 0.2 to 1.0 ha encompassing the majority of the managed cluster. Canopy closure and herbaceous cover varied from 0 to >70%.

Bird Surveys.—We sampled grassland birds using flush net surveys. Surveys were conducted on fixed-width transects between 28 November and 28 February in 2007–2008 and 2008–2009. Bird Surveys.—We sampled grassland birds using flush net surveys. Surveys were conducted on fixed-width transects between 28 November and 28 February in 2007–2008 and 2008–2009. We sampled 16 sites the first winter and 11 different sites the second year. Each site was sampled three times per winter except for three that were burned before the third round of sampling. All sites sampled the same year were >500 m apart. Our flush netting protocol was modified from Shackleford et al. (2001) and Carrie et al. (2002) as described by Brooks (2010). When a bird was flushed, it was identified to species if possible. If identification was uncertain, we would attempt to capture the bird for identification following the capture technique described in Bechtoldt and Stouffer (2005). We used the same sampling method in RCW stands, but made multiple systematic, non-overlapping passes through plots until they were completely sampled. Grassland birds that could not be identified to species were excluded from species-specific analyses but were included in analysis of total grassland bird density.

Vegetation Sampling.—We sampled vegetation structure and plant species composition at each site. Each 20-m wide transect in sites with transects was partitioned into 20-m intervals for vegetation sampling plots. We measured canopy closure in each plot using a spherical densitometer (Lemmon 1956), and basal area with a 10-factor prism (Avery 1967) and Biltmore stick (Jackson 1911). We measured herbaceous and woody plant density using a randomly placed 3-cm diameter pole (Wiens 1974), and modal herbaceous and woody heights within 30-cm of the pole were visually estimated to the nearest decimeter. We used a randomly placed 1-m² frame to estimate percent cover of herbaceous and woody ground vegetation, and species composition. We estimated the number of woody stems at ground level inside each 1-m² frame. We later grouped plant species into 15 guilds by combinations of life form (graminoid, forb, or woody) and U.S. Fish and Wildlife Service Wetland Indicator Status (WIS) (USDI 1988) to reduce the number of variables. We collected the same vegetation data for RCW clusters using 5–10 randomly placed sampling plots per cluster. Two 1-m² frame and four pole measurements were taken in each sampling plot for all stand types. Many of our study sites had patchy distributions of herbaceous cover and shrubs. We used the coefficient of variation (CV) to measure patchiness for herbaceous cover, woody cover, and herbaceous density among points in each transect (Wiens 1974). The CV was calculated using each individual mea-
surement within a site and represents heterogeneity, or patchiness, within a study site.

Statistical Analyses.—Individual stands were treated as the sample unit for all analyses. We calculated the number of birds flushed per hectare in each survey and averaged these densities from all surveys at each site. Vegetation sampling plots also were averaged over each site. We omitted one site classified as “other” and four sites that were >2 growing seasons since fire for analyses comparing bird densities and vegetation variables among stand types. Omitting these samples removed variation introduced by differences in time since fire among sites. Nineteen of the remaining 22 sites were one growing season since fire and three (1/stand type) were two growing seasons since fire. Six of these sites were upland stands, six were RCW stands, and 10 were bogs. All analyses were performed with SAS Version 9.2 (SAS Institute 2006).

We used log-linear generalized models to test for differences in densities of each species and total grassland birds among stand types. Henslow’s Sparrows did not occur in one stand type, and Bachman’s Sparrows did not occur in another; we tested for differences in densities only between stand types in which these species occurred. We specified a Poisson distribution for Sedge Wren and a negative binomial distribution for Bachman’s Sparrow, Henslow’s Sparrow, and total bird densities, both of which are appropriate for zero-rich data. Appropriate distributions were selected by estimating an overdispersion factor (\(c = \frac{\chi^2}{df}\)) and choosing the distribution with \(c\) closest to 1.0. All models had \(c \leq 1.02\) and were not overdispersed (Burnham and Anderson 2002). We used a significance level of 0.05 for all tests.

We conducted principal components analyses (PCA) to reduce the number of correlated vegetation structure variables and plant species composition guilds to fewer, uncorrelated principal components (PCs). We performed one PCA of vegetation structure variables using the \(n = 22\) data set and two other PCAs with the complete data set (\(n = 27\)), one on vegetation structure, and another on plant species guilds. We used varimax rotations to aid in interpretation of the PCs and retained all PCs with Eigenvalues >1. We used the \(n = 22\) PCs to examine vegetation structure differences among stand types; the \(n = 27\) PCs were used to model bird occurrence. We used MANOVA to test for differences in vegetation structure PC scores among stand types (\(n = 22\)). Pairwise differences between means were tested using Tukey–Kramer tests. Residuals were tested for normality using Shapiro–Wilks’ tests.

We used logistic regression to model the probability of Henslow’s Sparrow and Sedge Wren occurrence based on vegetation variables. We used the entire data set (\(n = 27\)) and its corresponding PCs for these analyses. We used the vegetation structure and plant guild PCs as independent predictor variables in an information-theoretic model selection approach (Burnham and Anderson 2002). The third plant PC was highly correlated with a vegetation structure PC and was not used when constructing candidate models. Henslow’s Sparrow and Sedge Wren global models were assessed for overdispersion (\(c = 1.40\) and 1.13, respectively). Models were ranked using Akaike’s Information second-order Criterion (AICc) for small sample size (Burnham and Anderson 2002). Models with \(\Delta\)AICc < 2 were considered the best models (Burnham and Anderson 2002). We also calculated an \(r^2\) General Information Criterion (\(r^2_{GIC}\)) for each model (Wright 2001). This is a pseudo \(r^2\) calculated from any one of the common information criteria and represents the relative proportional variance explained by a model.

RESULTS

Henslow’s Sparrows occurred at 11 of 27 study sites, Sedge Wrens at nine, and Bachman’s Sparrows at five sites. Henslow’s Sparrow densities were highest across all sites, followed by Bachman’s Sparrow and Sedge Wren. Densities of each species, considering only the sites where they occurred, were: Henslow’s Sparrow = 0.52–13.33, Sedge Wren = 0.42–3.03, and Bachman’s Sparrow = 0.42–2.22 birds/ha. The highest densities of Henslow’s Sparrows occurred on a 0.2-ha transect in a small (< 1 ha) bog. Grassland birds that could not be identified to species (e.g., Ammodramus spp. or other emberizids) accounted for 6% (5 birds) of the total bird density across all stand types combined. We did not model Bachman’s Sparrow occurrence because this species was detected at so few sites.

Bird Differences Among Stand Types.—Grassland bird densities in upland, RCW, and bog stands varied among species (Fig. 1). Bachman’s Sparrows were not detected in bog stands, and densities did not differ between upland and RCW stands (\(F_{1,10} = 0.33, P = 0.58\)). Henslow’s
Bachman’s Sparrow  
Henslow’s Sparrow  
Sedge Wren  
All species

**Fig. 1.** Mean (± SE) densities (birds/ha) for three species of wintering grassland birds and all species combined in DeSoto National Forest, Mississippi.

Sparrows were not detected in upland stands, and densities did not differ between bog and RCW stands ($F_{1,14} = 0.91, P = 0.36$). Sedge Wren densities did not differ among stand types ($F_{2,19} = 0.38, P = 0.69$). There were no differences in total grassland bird density among stand types ($F_{2,19} = 3.12, P = 0.068$), but density was highest in bogs (Fig. 1).

**PCA of Vegetation Structure.**—PCA of the vegetation structure variables with the $n = 22$ data resulted in three PCs with Eigenvalues $>1$, representing 84% of the variance (Table 1). The first PC represented woody understory structure and was mostly correlated with all woody understory structure variables and herbaceous height. The second PC represented herbaceous structure and was mostly correlated with the remaining herbaceous structure variables and woody cover CV. The third PC represented tree density and was mainly correlated with canopy closure and tree basal area.

PCA of the vegetation structure variables with the total data set ($n = 27$) resulted in three PCs with Eigenvalues $>1$, representing 82% of the variance (Table 2). PCs followed the pattern of the $n = 22$ analysis (Table 1). The first PC represented woody understory structure, the second represented herbaceous structure, and the third represented tree density. PCA of the plant species composition guilds resulted in five PCs with Eigenvalues $>1$, representing 70% of the variance (Table 3).

**Vegetation Structure Differences Among Stand Types.**—MANOVA revealed mean vegetation structure PC value differences among stand types ($\lambda = 0.23, F_6, 34 = 6.18, P < 0.001$). Herbaceous structure was higher in bogs than in upland ($P < 0.001$) and RCW stands ($P < 0.001$; Fig. 2); thus, bog stands had more continuous herbaceous cover and patchier woody cover. There were no significant differences in means for the woody structure PC, but RCW stands had a lower mean value. The tree density PC was not significantly different among stand types.

**Henslow’s Sparrow Models.**—Henslow’s Sparrow occurrence was best predicted by decreasing herbaceous density CV and increasing cover of the sedge *Scleria muhlenbergii* (Table 4). The best model was the only one with $\Delta$AICc $< 2$ and explained 39% of the relative proportional variation. The null model had $\Delta$AICc $= 13.50$. Parameter estimates for both variables in the best model had 95% confidence intervals that contained zero, indicating that, although there was an effect, the extent of the effect could not be quantified. Abnormally large parameter estimates resulting from logistic regression may occur due to small sample sizes (Nemes et al. 2009). The parameter estimate and standard error for *Scleria muhlenbergii* cover was $\beta = 10.75 ± 6.67 (95\% \text{ CI} = -3.0-24.51)$. The estimate for the herbaceous density CV was $\beta = -0.10 ± 0.05 (95\% \text{ CI} = -0.21-0.02)$.

**Sedge Wren Models.**—Sedge Wren occurrence was best predicted by decreasing tree basal area and increasing woody understory vegetation structure PC values (Table 5). No other models had $\Delta$AICc $< 2$. The null model had $\Delta$AICc $= 4.99$ and the best model explained only 17% of the relative proportional variation. The parameter estimate and standard error for the woody understory PC was $\beta = 1.22 ± 0.63 (95\% \text{ CI} = -0.07-2.51)$. The best model had $\Delta$AICc $= 8.51$. Parameter estimates were not significantly different among stand types.
TABLE 1. Rotated principal components pattern from a PCA of 12 vegetation structure variables (n = 22) used to compare vegetation among three stand types. Values are the correlations of the raw variables with each PC. Highest correlations are in bold. CV = coefficient of variation.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Woody PC</th>
<th>Herb PC</th>
<th>Tree PC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woody cover</td>
<td>0.896</td>
<td>-0.268</td>
<td>0.270</td>
</tr>
<tr>
<td>Woody density</td>
<td>0.885</td>
<td>-0.279</td>
<td>-0.154</td>
</tr>
<tr>
<td>Number stems</td>
<td>0.857</td>
<td>-0.305</td>
<td>0.024</td>
</tr>
<tr>
<td>Woody height</td>
<td>0.738</td>
<td>-0.570</td>
<td>0.157</td>
</tr>
<tr>
<td>Herb height</td>
<td>0.651</td>
<td>-0.222</td>
<td>0.115</td>
</tr>
<tr>
<td>Herb density</td>
<td>-0.191</td>
<td>0.935</td>
<td>-0.125</td>
</tr>
<tr>
<td>Herb cover</td>
<td>-0.386</td>
<td>0.835</td>
<td>-0.035</td>
</tr>
<tr>
<td>Woody cover CV</td>
<td>-0.571</td>
<td>0.632</td>
<td>-0.068</td>
</tr>
<tr>
<td>Herb cover CV</td>
<td>0.613</td>
<td>-0.693</td>
<td>0.276</td>
</tr>
<tr>
<td>Herb density CV</td>
<td>0.550</td>
<td>-0.737</td>
<td>0.072</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>0.136</td>
<td>0.091</td>
<td>0.948</td>
</tr>
<tr>
<td>Tree basal area</td>
<td>0.009</td>
<td>-0.378</td>
<td>0.869</td>
</tr>
<tr>
<td>Proportion $s^2$ explained</td>
<td>61%</td>
<td>14%</td>
<td>9%</td>
</tr>
</tbody>
</table>

-0.08 - 2.51). The estimate for basal area was $-6.99 \pm 3.25$ (95% CI = $-13.71$ – 0.28).

DISCUSSION

Most upland stands supported low numbers of grassland birds (< 1 bird/ha), but the presence of Henslow's Sparrows in RCW and bog stands led to densities >3 birds/ha. This type of information is important because it provides baseline knowledge of which habitat types may be most important for birds. Species-specific preferences should be considered, however, as two of our three study species did not occur in all three stand types. Our small sample sizes may have limited revealing significant differences between birds and vegetation among stand types.

Bachman's Sparrows occurred in upland and RCW stands but not in bog stands in our winter study. These results support the breeding season observations of Allen et al. (2006), who reported Bachman's Sparrows to be more common in upland habitats compared to wetter pocosins in North Carolina. Haggerty (1998) suggested breeding Bachman's Sparrows may prefer patchy herbaceous ground cover because this facilitates prey capture by foraging birds. Cox and Jones (2009) reported Bachman's Sparrow winter abundances at sites in Georgia were positively correlated with bare ground and negatively correlated with increased grass structure and shrubs <1 m in height. Upland stands in DSNF have patchy herbaceous cover, and Bachman's

TABLE 2. Rotated principal components pattern from a PCA of 12 vegetation structure variables (n = 27) used to model Henslow's Sparrow and Sedge Wren occurrence. Values are the correlations of the raw variables with each PC. Highest correlations are in bold. CV = coefficient of variation.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Woody PC</th>
<th>Herb PC</th>
<th>Tree PC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woody density</td>
<td>0.902</td>
<td>-0.166</td>
<td>0.037</td>
</tr>
<tr>
<td>Woody cover</td>
<td>0.884</td>
<td>-0.155</td>
<td>0.383</td>
</tr>
<tr>
<td>Number of stems</td>
<td>0.819</td>
<td>-0.313</td>
<td>0.055</td>
</tr>
<tr>
<td>Woody height</td>
<td>0.815</td>
<td>-0.319</td>
<td>0.256</td>
</tr>
<tr>
<td>Herb cover CV</td>
<td>0.693</td>
<td>-0.553</td>
<td>0.379</td>
</tr>
<tr>
<td>Herb height</td>
<td>0.580</td>
<td>-0.236</td>
<td>-0.025</td>
</tr>
<tr>
<td>Woody cover CV</td>
<td>-0.693</td>
<td>0.468</td>
<td>-0.158</td>
</tr>
<tr>
<td>Herb density</td>
<td>0.163</td>
<td>0.943</td>
<td>-0.096</td>
</tr>
<tr>
<td>Herb cover</td>
<td>-0.480</td>
<td>0.773</td>
<td>-0.166</td>
</tr>
<tr>
<td>Herb density CV</td>
<td>0.529</td>
<td>-0.755</td>
<td>0.151</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>0.122</td>
<td>-0.031</td>
<td>0.922</td>
</tr>
<tr>
<td>Tree basal area</td>
<td>0.118</td>
<td>-0.230</td>
<td>0.888</td>
</tr>
<tr>
<td>Proportion $s^2$ explained</td>
<td>60%</td>
<td>13%</td>
<td>9%</td>
</tr>
</tbody>
</table>
TABLE 3. Rotated principal components pattern from a PCA of 15 plant species composition guilds \((n = 27)\) used in the model to predict Henslow’s Sparrow and Sedge Wren occurrence. Values are the correlations of the raw variables with each PC. Highest correlations are in bold. Gram is graminoid. Uppercase abbreviations refer to USFWS Wetland Indicator Status (USDI 1988). OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, and UPL = upland.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC I</th>
<th>PC II</th>
<th>PC III</th>
<th>PC IV</th>
<th>PC V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gram FAC</td>
<td>0.813</td>
<td>-0.267</td>
<td>-0.048</td>
<td>-0.049</td>
<td>0.028</td>
</tr>
<tr>
<td>Gram FACU</td>
<td>0.804</td>
<td>-0.323</td>
<td>0.095</td>
<td>-0.152</td>
<td>-0.114</td>
</tr>
<tr>
<td>Woody FACU</td>
<td>0.549</td>
<td>-0.090</td>
<td>0.152</td>
<td>0.204</td>
<td>-0.347</td>
</tr>
<tr>
<td>Gram UPL</td>
<td>-0.746</td>
<td>-0.266</td>
<td>0.174</td>
<td>-0.200</td>
<td>-0.117</td>
</tr>
<tr>
<td>Gram FACW</td>
<td>-0.751</td>
<td>0.133</td>
<td>-0.311</td>
<td>-0.222</td>
<td>0.000</td>
</tr>
<tr>
<td>Woody OBL</td>
<td>-0.129</td>
<td>0.927</td>
<td>0.068</td>
<td>-0.042</td>
<td>-0.053</td>
</tr>
<tr>
<td>Forb FACW</td>
<td>-0.155</td>
<td>0.871</td>
<td>-0.117</td>
<td>-0.033</td>
<td>0.022</td>
</tr>
<tr>
<td>Woody FACW</td>
<td>-0.061</td>
<td>-0.139</td>
<td>0.862</td>
<td>-0.058</td>
<td>0.240</td>
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<tr>
<td>Woody FAC</td>
<td>0.073</td>
<td>0.139</td>
<td>0.744</td>
<td>0.186</td>
<td>-0.353</td>
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<tr>
<td>Forb OBL</td>
<td>-0.582</td>
<td>0.052</td>
<td>-0.640</td>
<td>-0.034</td>
<td>0.032</td>
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<tr>
<td>Forb UPL</td>
<td>-0.062</td>
<td>0.084</td>
<td>0.055</td>
<td>0.808</td>
<td>-0.013</td>
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<tr>
<td>Woody UPL</td>
<td>0.169</td>
<td>-0.097</td>
<td>-0.041</td>
<td>0.684</td>
<td>-0.293</td>
</tr>
<tr>
<td>Forb FACU</td>
<td>0.175</td>
<td>-0.149</td>
<td>0.140</td>
<td>0.491</td>
<td>0.353</td>
</tr>
<tr>
<td>Forb FAC</td>
<td>0.024</td>
<td>-0.071</td>
<td>0.069</td>
<td>-0.050</td>
<td>0.850</td>
</tr>
<tr>
<td>Gram OBL</td>
<td>-0.235</td>
<td>0.352</td>
<td>-0.371</td>
<td>-0.082</td>
<td>0.512</td>
</tr>
<tr>
<td>Proportion s² explained</td>
<td>28%</td>
<td>12%</td>
<td>11%</td>
<td>10%</td>
<td>9%</td>
</tr>
</tbody>
</table>

Sparrows were at least tolerant of this cover type during both breeding and nonbreeding seasons, although an adequate level of graminoid cover is important for stand occupancy (Brooks and Stouffer 2010). Bachman’s Sparrows are often associated with areas of dense herbaceous cover and low shrub cover (Plentovich et al. 1998b, Tucker et al. 2004), but they may be flexible in their habitat preferences. Haggerty (2000) conducted a region-wide study across five states and found Bachman’s Sparrow preferences for forb cover, vegetation height, and tree density varied widely across regions.

We found Bachman’s Sparrows used two of the six clusters managed for RCWs (Dunning and Watts 1990, Wilson et al. 1995). Plentovich et al. (1998b) also found that not all RCW clusters surveyed at sites in Florida were suitable for Bachman’s Sparrows. One explanation is the relatively small size of many RCW clusters. The mean breeding season home-range size of Bachman’s Sparrow is between 1.5 and 4.8 ha, and varies with time since fire, timber age, and vegetation structure (Haggerty 1998, Stober and Krementz 2006, Cox and Jones 2007). Many, but not all, RCW clusters in DSNF are probably too small (<0.5 ha) to be of value to Bachman’s Sparrows, particularly if the surrounding habitat is inadequate. Winter home range size, however, has not been well studied.

There may be several reasons why Bachman’s Sparrows avoided bogs. Bogs often contain standing water (Folkerts 1982), and some species of ground-dwelling birds may prefer drier habitats. Another reason is that most bogs in DSNF have either few trees or a closed canopy of pine. Stands with high tree densities are generally avoided by Bachman’s Sparrows (Haggerty 1998, 2000), and open bog stands may lack adequate singing perches, which are important habitat features (Dunning and Watts 1990, Gobris 1992, Brooks and Stouffer 2010). Perches may indicate appropriate habitat, even in winter, if...
birds maintain territories throughout the year (Cox and Jones 2009). Damage from Hurricane Katrina in 2005 disproportionately affected mature upland stands in DSNF, possibly improving upland stand habitat quality for Bachman’s Sparrows. The hurricane thinned canopies, simultaneously producing downed tree crowns and upturned root balls. Bachman’s Sparrows sing from downed crowns and may use root balls for escape; absence of these features reduces breeding season occupancy by Bachman’s Sparrows (Brooks and Stouffer 2010) and could affect winter habitat use. Henslow’s Sparrows were detected only in bog and RCW stands. These sparrows, in the Gulf Coastal Plain, seem to prefer some grassland habitats over others. Plentovich et al. (1999), working in pitcher plant bogs and upland pine stands in Alabama, only found Henslow’s Sparrows in bogs and transition zones between bog and upland pine habitats. Tucker and Robinson (2003) also found Henslow’s Sparrows using small bogs in upland pine habitat in winter along the Gulf Coast. Other studies, however, have found high densities of Henslow’s Sparrows in upland longleaf pine habitats (Carrie et al. 2002, Johnson 2006, Palasz et al. 2010), but many of these sites were well-managed with fire and not adjacent to bogs. The primary reason Henslow’s Sparrows avoided upland habitats in DSNF is probably the lack of a dense, continuous herbaceous layer, reflected by inclusion of the herbaceous density CV in the best habitat model, even in stands regularly managed with fire. The majority of the upland stands we sampled had experienced only one growing season since fire, a condition that should favor Henslow’s Sparrows (Carrie et al. 2002, Bechtoldt and Stouffer 2005). These stands had an herbaceous layer, but it was
TABLE 5. Candidate models used to model Sedge Wren occurrence. Plant1–Plant5 are principal components of the plant species guilds. Herb = herbaceous structure, Wood = woody understory structure, and Tree = tree density.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>AAICc</th>
<th>(w_i)</th>
<th>(\hat{c}_{AICc})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood PC + Basal area</td>
<td>28.08</td>
<td>0.00</td>
<td>0.07</td>
<td>0.17</td>
</tr>
<tr>
<td>Basal area</td>
<td>30.49</td>
<td>2.41</td>
<td>0.06</td>
<td>0.09</td>
</tr>
<tr>
<td>Wood PC + Canopy closure</td>
<td>30.59</td>
<td>2.52</td>
<td>0.06</td>
<td>0.09</td>
</tr>
<tr>
<td>Herb PC + Tree PC</td>
<td>30.93</td>
<td>2.86</td>
<td>0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>31.00</td>
<td>2.93</td>
<td>0.06</td>
<td>0.07</td>
</tr>
<tr>
<td>Wood PC + Herb PC + Tree PC</td>
<td>31.24</td>
<td>3.17</td>
<td>0.06</td>
<td>0.07</td>
</tr>
<tr>
<td>Wood PC</td>
<td>32.73</td>
<td>4.65</td>
<td>0.05</td>
<td>0.01</td>
</tr>
<tr>
<td>Null</td>
<td>33.06</td>
<td>4.99</td>
<td>0.05</td>
<td>0.00</td>
</tr>
<tr>
<td>Plant5</td>
<td>33.56</td>
<td>5.48</td>
<td>0.05</td>
<td>-0.02</td>
</tr>
<tr>
<td>Herb PC + Plant4</td>
<td>34.59</td>
<td>6.51</td>
<td>0.05</td>
<td>-0.08</td>
</tr>
<tr>
<td>Plant2</td>
<td>35.10</td>
<td>7.03</td>
<td>0.05</td>
<td>-0.08</td>
</tr>
<tr>
<td>Wood PC + Herb PC</td>
<td>35.16</td>
<td>7.09</td>
<td>0.05</td>
<td>-0.08</td>
</tr>
<tr>
<td>Herb PC</td>
<td>35.30</td>
<td>7.22</td>
<td>0.05</td>
<td>-0.09</td>
</tr>
<tr>
<td>Plant1</td>
<td>35.39</td>
<td>7.31</td>
<td>0.05</td>
<td>-0.09</td>
</tr>
<tr>
<td>Wood PC + Plant4 + Wood PC*Plant4</td>
<td>35.95</td>
<td>7.87</td>
<td>0.04</td>
<td>-0.11</td>
</tr>
<tr>
<td>Plant1 + Plant5</td>
<td>36.09</td>
<td>8.01</td>
<td>0.04</td>
<td>-0.12</td>
</tr>
<tr>
<td>Plant2 + Plant4</td>
<td>36.77</td>
<td>8.69</td>
<td>0.04</td>
<td>-0.15</td>
</tr>
<tr>
<td>Plant1 + Plant4</td>
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<td>8.97</td>
<td>0.04</td>
<td>-0.16</td>
</tr>
<tr>
<td>Plant1 + Plant2</td>
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<td>9.55</td>
<td>0.04</td>
<td>-0.18</td>
</tr>
<tr>
<td>Plant1 + Plant2 + Plant4 + Plant5</td>
<td>40.69</td>
<td>12.61</td>
<td>0.04</td>
<td>-0.33</td>
</tr>
<tr>
<td>Global</td>
<td>46.86</td>
<td>18.78</td>
<td>0.03</td>
<td>-0.67</td>
</tr>
</tbody>
</table>

too patchy to provide suitable habitat. These results demonstrate that fire history alone may not predict sparrow occurrence in pine savannas. Henslow's Sparrows will use both upland longleaf pine savannas and bogs in some areas, but apparently prefer bogs when surrounding upland habitat is of marginal quality, as is the case in DSNF. Small-scale bog restoration may be important for Henslow's Sparrows in these areas.

Henslow's Sparrow stand occurrence in DSNF was best predicted by increasing continuous, spatially homogenous herbaceous density, which is also reflected by their avoidance of upland stands. Our results support those of Rotenberry and Wiens (1980) who found abundance of tallgrass prairie birds, including breeding Henslow's Sparrows, was negatively correlated with ground cover heterogeneity. Patchy herbaceous structure can have negative effects on grassland birds in multiple ways (Shriver 1996, Perkins and Vickery 2001, Thatcher et al. 2006).

Cover of the sedge Scleria muhlenbergii increased the probability of Henslow's Sparrow stand occurrence. This sedge can reach >50% cover in some bogs in DSNF but does not occur in upland stands. All bogs that had high densities of Henslow's Sparrows also had high cover of S. muhlenbergii. Scleria is an annual that senesces achenes in autumn (W. J. Platt, pers. comm.), and the seeds are available to ground-foraging birds in early winter. Species of Scleria have been found to be important in Henslow's Sparrow diets in Mississippi and Louisiana (Fuller 2004, DiMiceli 2006). Scleria muhlenbergii could be important for identifying high-quality habitat if Henslow's Sparrows use habitat cues to select wintering areas upon fall arrival. Scleria muhlenbergii responds strongly to fire and is most abundant the first growing season after fire, but decreases substantially by the following season in the absence of fire (W. J. Platt, pers. comm.).

Henslow's Sparrow use of RCW stands was ephemeral. Mean Henslow's Sparrow density in RCW stands declined from 3.5 birds/ha in late November to 0.6 in early January (Brooks 2010). Henslow's Sparrows are site faithful during the core months of winter (Dec–Feb) (Plentovich et al. 1998a, Thatcher et al. 2006, Johnson et al. 2009). Our results suggest temporary use of RCW stands by transient birds that had not settled on winter territories, a result that corresponds to movements described in Louisiana (Johnson et al. 2009). RCW stands in DSNF had lower herbaceous structure than bog stands, indicating the habitat was of lower quality than bogs, where densities did not significantly decline during the
year of sampling (Brooks 2010). Patch size could be one reason why birds did not remain in RCW stands. Henslow’s Sparrows occupy small habitat patches in high-quality bogs but could be more area sensitive in lower-quality habitats.

Sedge Wrens occurred in all stand types, and densities did not differ among stand types. We found only one Sedge Wren in one RCW stand; this species was not detected in two other studies of winter bird communities in RCW clusters (Conner et al. 2002, Provencher et al. 2002). Our modeling of stand occurrence based on vegetation variables weakly suggests Sedge Wrens in DSNF may prefer woody understory vegetation. Woody understory vegetation is abundant in all stand types in DSNF but is lowest in RCW clusters. Our results do not show statistically fewer Sedge Wrens and lower woody structure in RCW clusters, perhaps because of our small sample size, but we suspect that further sampling may reveal differences.

Sedge Wren site occurrence was best predicted by decreasing tree basal area and increasing woody understory vegetation structure. The many habitat types used by Sedge Wrens across the Southeast show they are habitat generalists in wintering areas (Lowery 1974, Imhof 1976, Baldwin et al. 2007). Thus, it is not surprising the best model explained only 17% of the relative proportional variation. Our finding of Sedge Wren preference for woody understory contrasts with Baldwin et al. (2007), the only other quantitative study of Sedge Wren winter habitat preference. Site occupancy and abundance in their study were not associated with shrub densities but with dense herbaceous vegetation. However, they worked in Texas coastal prairies, an entirely different ecosystem than pine savannas. Sedge Wrens are insectivorous (Herkert et al. 2001), and insect abundance also could be an important driver of habitat selection.

Caution must be used when interpreting trends observed during this study because they are based on only two seasons of observations. We believe, however, the conditions in DSNF during the study influenced the observed habitat-type preferences of the study species. These habitats change rapidly between years and after fire; thus, quality of habitat types will be in flux, and specific habitats may appeal to birds differently between years. Our best habitat models were not substantially better than null models, and the parameter estimates had large confidence intervals. These models may not be suitable for prediction, but are suggestive of potentially important associations warranting further research.

We did not include weather data in our analyses. We observed a gradual decline in Henslow’s Sparrow and Sedge Wren densities over sampling events in the first sampling year (Brooks 2010). We speculate this was due to lower-than-average precipitation the previous growing season, which could lead to increased predation and fewer seed resources (Pulliam and Parker 1979, Thatcher et al. 2006). Precipitation in DSNF in 2007 was 4-159 mm below average every month from March to November except for October (85 mm above average), while the 2008 growing season received an even mixture of above- and below-average precipitation (USDC 2009).

CONSERVATION IMPLICATIONS

Many areas that appear suitable for Henslow’s Sparrows, particularly upland longleaf pine savannas, are unsuitable because of the patchy distribution of herbaceous vegetation. Restoring the herbaceous component of longleaf pine savannas to a continuous layer should be one of the principal goals for those interested in grassland bird conservation. Upland stands are suitable for Bachman’s Sparrows and Sedge Wrens in DSNF and, if restored, may become suitable for Henslow’s Sparrows. This sparrow occasionally occupies isolated patches of upland habitat, but the general trend in many areas is a preference for bogs. Bogs can be maintained with tree thinning and prescribed fire, but upland stands require reduction in shrub cover, which will not happen with fire alone. It may require a combination of fire, mechanical removal, and herbicide application (Boyer 1992, Olson and Platt 1995, Drewa et al. 2002b). Small-scale bog restoration for Henslow’s Sparrow is likely the most effective management strategy. Many practices currently used in DSNF benefit grassland birds via ecosystem restoration (e.g., prescribed fire, a shift towards more growing-season fires, and slash pine removal in bogs). Increasing the size and number of RCW clusters also will increase the area of potentially suitable habitats for all three grassland bird species.

ACKNOWLEDGMENTS

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ABSTRACT.—We studied sound emission in the non-oscine Cuban Tody (Todus multicolor) to quantify its acoustic repertoire and to document geographic variation in its songs across the Cuban archipelago. Cuban Todies emitted three types of sounds. The characteristic song of the species was recorded from 98% of 116 individuals. The characteristic song and a variant form recorded from two individuals consisted of trains of multi-harmonic short, downward frequency modulated notes emitted at peak frequencies below 4 kHz. A third type of sound in the limited repertoire of the species recorded from two birds is presumably produced with the wings and appears in the spectrograms as a train of short clicks with frequencies also below 4 kHz. Evidence of geographic variation was found in the characteristic song. Birds from Isla de la Juventud and Pinar del Rio emitted more notes per train spaced at longer intervals than birds from the rest of the provinces. The peak frequency of the notes had lower values in birds from Isla de la Juventud. A discriminant function analysis grouped todies from different provinces into two main clusters corresponding to western Cuba and eastern Cuba. This geographic song variation may indicate genetic differences in this sedentary forest bird, and the existence of two "incipient species" of todies in Cuba. Isolation may have been caused by discontinuities in the mainland of Cuba that occurred between the Pleistocene and Holocene or by deforestation occurring in Cuba for the last five centuries. Received 5 January 2010. Accepted 19 October 2010.

Geographical variation should be considered when analyzing vocal repertoires of birds, as species distributed across wide areas may vary in their songs. Geographic variations have been reported mostly from oscines (Mundinger 1982, Martens 1996), but also from non-oscines (Goldstein 1978, Saunders 1983, Bretagnolle 1989, Wright 1996) and suboscine taxa (Isler et al. 1998, Lindell 1998, Isler et al. 1999). Several theories have been proposed to explain the geographic variation in vocalizations observed in different species. Geographic variations may result from adaptation to local conditions, such as social or structural environments (Lemon 1975, Payne 1980), but also from non-adaptive processes such as the accumulation of genetic or cultural mutations in a population due to isolation or founder events (Tack et al. 2005), or some combination of genetic variation and learning (Kroodsma 1996). Geographic variation in vocalizations is expected to be reinforced by limited intermixing between the species’ populations due to geographic isolation. Thus, geographic song variation may reflect structure among populations of a species.

The Cuban Tody (Todus multicolor) belongs to a genus of charismatic small and colorful non-oscine birds endemic to the Caribbean, represented by two species in Hispaniola, one in Jamaica, one in Puerto Rico, and one in Cuba (Raffaele et al. 1998). The Cuban Tody is well distributed in Cuba and is common in semi-deciduous mesophytic forest and coastal vegetation (Garrido and Kirkconnell 2000), swamp vegetation complex (Gonzalez et al. 1997), and secondary vegetation (Gonzalez et al. 2001). This species perches for long periods, often bobbing its head up and down while locating the small adult and larval insects, and spiders upon which it feeds. The sedentary behavior, forest use, and short distance flight of this species suggest easier isolation of populations due to deforestation, a phenomenon that has occurred in Cuba during the last five centuries (Fig. 1). It may be advantageous to study the song repertoire of the Cuban Tody since, among many non-oscines, songs are not learned from other individuals (Konishi and Nottebohm 1969, Kroodsma 1989), and vocal behavior may be used as an unambiguous genetic marker for an individual.

Cuba, the largest archipelago of the Greater Antilles, is <150 km wide but extends east-west for >1,000 km. We tested the hypothesis that the song of the Cuban Tody exhibits geographic variation across the length of Cuba by characterizing the acoustic repertoire of the species from individuals recorded in seven provinces representative of the island. We specifically predicted that song similarity should be inversely related to
distance between individuals. There are no acoustic studies of the Cuban Tody. Thus, to test this prediction, we recorded the song of the species across Cuba, characterized it quantitatively, and examined geographic variation in songs by using a discriminant function analysis.

METHODS

Field Recordings.—Acoustic recordings of the Cuban Tody were obtained between 2001 and 2006 at 15 sites in seven provinces of Cuba: Isla de la Juventud (1 site), Pinar del Río (3), Matanzas (4), Ciego de Ávila (1), Camagüey (1), Santiago de Cuba (1), and Guantánamo (4) (Fig. 1). Recordings were made from February to August to include most of the reproductive period of the species (Garrido and Kirkconnell 2000).

We recorded songs from 116 solitary adults perching in the forest up to 10 m from the microphone. Adults are easily recognized because they combine the ventral pale gray color with a brilliant red throat patch that is absent in young, which are entirely pale gray below (Garrido and Kirkconnell 2000). We could not test for vocal differences between males and females as they can not be identified by plumage (Raffaele et al. 1998, Garrido and Kirkconnell 2000). Recordings were made using a Marantz PMD 222 tape recorder and Sennheiser ME66/K6 microphone. Care was taken to avoid signal saturations and to maximize signal-to-noise ratio.

Acoustic Analysis.—A data base of 1,371 songs (11.67 ± 4.52 songs/bird) including 8,885 notes was analyzed. Songs were digitized to examine the quality of the recordings with 16 bit accuracy and a sampling rate of 44,100 Hz using BatSound, Version 2.1 (Petterson Elektronic AB, Uppsala, Sweden). A note was defined as a continuous tracing on a spectrogram following Nelson et al. (1996), while a song was defined following Baptista (1974) and Staicer (1989) as an arrangement of notes forming a coherent unit. Songs were analyzed with Avisoft-SAS Lab Pro 4.3 (Avisoft Bioacoustics, Berlin, Germany). Spectrograms were made using consecutive Fast Fourier Transforms (FFT’s) and Hamming windows with a 92% overlap. A 512 points FFT was chosen to attain a frequency resolution of 86 Hz and a time resolution of 0.18 msec.

We used an automatic two-threshold algorithm for note separation with the additional start/end threshold set at −20 dB. This algorithm minimizes the effect that different note amplitudes may have on the measurements. The following parameters were automatically measured: (1) note duration (time between start and end of a note measured in msec in the spectrogram), (2) peak frequency (frequency in kHz corresponding with the maximal intensity in the power spectrum), (3) initial and (4) final frequency (values of frequency measured, respectively, at the beginning and at end of the note), (5) bandwidth (calculated as the difference between the lower and higher values of frequency measured at 20 dB below peak intensity in the power spectrum), and (6) entropy (used as an estimate of the tonal-noisy structure of the note: zero for pure-tone signals and 1 for random noise). We counted the number of notes in each song and calculated the interval between notes and songs. All values of the acoustic parameters are given as means ± SD.
Statistical Analysis.—Statistical analysis was performed using Statistica Version 7.0 (StatSoft Inc. 2004). The data sets were normally distributed (Kolmogorov-Smirnov test, \( P > 0.05 \)) and we used parametric statistics (one-way ANOVA). Statistical differences between several mean values were analyzed with a Newman-Keuls post-hoc test (identical letters indicate no statistically significant difference between means). All analyses were conducted using mean values per individual and the level of significance was \( \alpha = 0.05 \).

A multivariate discriminant function analysis (DFA) was performed using SPSS Version 16.0 (SPSS, Chicago, IL, USA) with individuals as cases and number of notes, note duration, interval between notes, initial frequency, peak frequency, final frequency, and interval between songs as parameters. We used DFA to generate linear combinations of variables for assigning cases to their pre-determined groups (Quinn and Keough 2002).

RESULTS

Sounds Emitted.—The characteristic song (tot-tot-tot) of the Cuban Tody was present in >98% of the recordings in each province studied. It was emitted by single birds in most cases that alternated singing with feeding behavior. The song was repeated at time intervals of 0.04-15.62 sec and included 3-23 notes. Each note was downward frequency-modulated and often had a

**FIG. 2.** A. Oscillogram (above) and spectrogram (below) of a sequence of the characteristic song of the Cuban Tody. B. Detailed spectrogram (left) and power spectra (right) of the song marked in A with an asterisk.
The initial frequency of the fundamental harmonic varied from 3.89 to 3.49 kHz and the final frequency from 1.50 to 2.49 kHz. The acoustic parameters that characterized this song in each province varied (Table 1). A variant form of the characteristic song of the Cuban Tody was detected in two individuals, one in Pinar del Rio and one in Santiago de Cuba. Each time, the song accompanied conspecific aggressive behavior and chasing, and sounded like trrrrrrrrr-trrrrrrrrrrrr. This song variant in the spectrogram resembles the characteristic song in that it is also a train of downward frequency-modulated notes (Fig. 3). This variant, compared to the characteristic song of the species, had a higher note repetition rate (average interval between notes of 23.53 ± 0.72 msec; n = 2 birds; 15 songs) and a lower frequency content of the fundamental harmonic (initial frequency: 2.72 ± 0.01 kHz; final frequency: 1.69 ± 0.03 kHz). The notes typically showed two harmonics.

Another sound emitted by the Cuban Tody was presumably produced with the wings and is responsible for the species popular name in Cuba “Pedorrera”, a Spanish onomatopoeic rendering of this sound (Garrido and Kirkconnell 2000). Perceived as a prrr-prrr, it was frequently emitted by birds interacting with conspecifics or heterospecifics invading their territory. The average sound (n = 2 birds) appears in the spectrogram like a train of more than four short clicks (click duration of 6.83 ± 1.22 msec) covering a frequency band between 3.34 ± 0.43 to 2.59 ± 0.18 kHz (Fig. 4).

**Variation in the Characteristic Song.**—Most acoustic parameters used to describe the characteristic song of the Cuban Tody had statistical differences among provinces. Birds from Isla de la Juventud and Pinar del Rio emitted more notes per train spaced at longer intervals than birds from the rest of the provinces. The peak frequency of the notes had lower values in birds from Isla de la Juventud. These differences, however, did not show monotonic changes along the island of Cuba, which was taken as evidence for absence of continuous variation (Table 1).

We applied a discriminant function analysis (DFA) to 116 individuals from seven provinces of Cuba to assess the presence of geographic song variation in the Cuban Tody. Individuals of Isla de la Juventud and Guantánamo were correctly (83.3%) classified to their provinces (Table 2). Correct classification in the rest of the provinces

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**Table 1.** Acoustic parameters (± SD) of the characteristic song of the Cuban Tody in each province studied. There were significant differences (One-way ANOVA, P < 0.05) among provinces for each parameter. Provinces are ordered from west to east.

<table>
<thead>
<tr>
<th>Locality</th>
<th>n</th>
<th>Number of notes</th>
<th>Duration (msec)</th>
<th>Interval song (sec)</th>
<th>Initial freq (kHz)</th>
<th>Final freq (kHz)</th>
<th>Bandwidth (kHz)</th>
<th>Peak freq (kHz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isla de la Juventud</td>
<td>24</td>
<td>11.9 ± 4.5a</td>
<td>17.6 ± 2.0b</td>
<td>111.3 ± 10.5a</td>
<td>3.60 ± 0.54a</td>
<td>3.78 ± 0.21a</td>
<td>8.22 ± 0.16a</td>
<td>1.75 ± 0.07a</td>
</tr>
<tr>
<td>Pinar del Río</td>
<td>8</td>
<td>3.2 ± 1.7b</td>
<td>5.2 ± 3.1b</td>
<td>5.2 ± 3.1b</td>
<td>3.78 ± 0.21a</td>
<td>3.88 ± 0.47a</td>
<td>11.5 ± 0.12a</td>
<td>3.01 ± 0.13a</td>
</tr>
<tr>
<td>Matanzas</td>
<td>13</td>
<td>5.3 ± 2.4b</td>
<td>6.0 ± 1.4b</td>
<td>10.17 ± 7.7b</td>
<td>3.88 ± 0.21a</td>
<td>4.11 ± 0.32a</td>
<td>18.7 ± 0.16a</td>
<td>3.91 ± 0.14a</td>
</tr>
<tr>
<td>Ciego de Ávila</td>
<td>9</td>
<td>5.3 ± 2.4b</td>
<td>6.0 ± 1.3b</td>
<td>10.17 ± 7.7b</td>
<td>3.88 ± 0.21a</td>
<td>4.11 ± 0.32a</td>
<td>18.7 ± 0.16a</td>
<td>3.91 ± 0.14a</td>
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<td>Camagüey</td>
<td>3</td>
<td>5.5 ± 3.2b</td>
<td>15.1 ± 1.4b</td>
<td>20.2 ± 1.1b</td>
<td>3.88 ± 0.21a</td>
<td>5.67 ± 0.35a</td>
<td>39.4 ± 0.16b</td>
<td>7.89 ± 0.14a</td>
</tr>
<tr>
<td>Santiago de Cuba</td>
<td>8</td>
<td>4.9 ± 1.3b</td>
<td>16.5 ± 1.3b</td>
<td>20.2 ± 1.1b</td>
<td>3.88 ± 0.21a</td>
<td>5.67 ± 0.35a</td>
<td>39.4 ± 0.16b</td>
<td>7.89 ± 0.14a</td>
</tr>
<tr>
<td>Guantánamo</td>
<td>50</td>
<td>3.8 ± 0.3b</td>
<td>17.7 ± 1.7a</td>
<td>86.8 ± 0.32a</td>
<td>3.76 ± 0.31a</td>
<td>17.0 ± 0.24a</td>
<td>23.0 ± 0.16a</td>
<td>5.00 ± 0.32a</td>
</tr>
</tbody>
</table>

*a, b, c = represent the results of a Newman-Keuls post hoc test with a different statistically from b, and b from c.
ranged between 0.0 to 38.5%. Individuals from Pinar del Río were statistically reassigned to Isla de la Juventud, while individuals from Matanzas and more eastern provinces were statistically reassigned to Guantánamo. Two individuals from Matanzas were reassigned to Pinar del Río and one from Ciego de Ávila was reassigned to Isla de la Juventud (Table 2; Fig. 5). A MANOVA showed the model was significant (Wilks’ $\lambda = 0.099$, $X^2 = 243.3$, df = 42, $P = 0.000$) and that 94.3% of the variation was explained by the two discriminant functions (Fig. 5). The proportion of correctly classified vocalizations by cross-correlation was 61.2%. The first discriminant function, which explained 86% of the variation, was more influenced by interval between notes and number of notes, while the second function was influenced by interval between songs and peak frequency (Table 3).

**DISCUSSION**

**Vocal Repertoire of the Cuban Tody.**—The 116 birds studied across the Island of Cuba emitted only three different types of calls. Two of these sounds, the characteristic song of the species and the sound presumably produced with the wings, have been previously described onomatopoetically (Raffaele et al. 1998, Garrido and Kirkconnell 2000). The variant form of the characteristic song had not been previously reported. Its similarities to the characteristic song could have been sufficient to consider both as the same by
The species repertoire size is comparable to other non-oscines such as *Percnostola saturata* (Braun et al. 2005), but smaller than that of *Todus mexicanus*, which exhibits six different song types in its repertoire (Kepler 1977).

Geographic Variation in the Characteristic Song of the Cuban Tody.—Our prediction of an inverse relation between song similarity and distance between individuals was partially supported by our findings. The characteristic song of the Cuban Tody exhibits two main forms on the archipelago of Cuba (Fig. 5), one corresponding to Western Cuba (Isla de la Juventud and Pinar del Rio) and the other to Eastern Cuba (from Guantánamo to Matanzas). Song variation can reflect historical barriers (Baril and Barlow 2000, Tack et al. 2005), and we see two possible explanations for the geographic variation that we observed in the Cuban Tody songs: one ancient and the other more recent. The Cuban area alternated between being one continuous island in the Pleistocene, which could propitiate a constant gene flow among the Cuban Tody populations, to several islands during periods of high sea level that might act as a physical barrier to this flow. Kepler (1977) used the fossil evidence presented by Olson (1976) to hypothesize that *Paleotodus* dispersed from the Yucatan Peninsula to Cuba during the Pleistocene or earlier and thereafter evolved into the Cuban species (Cuban Tody). Overton and Rhoads (2004), in agreement

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**FIG. 4.** A. Oscillogram (above) and spectrogram (below) of the sound produced with the wings by the Cuban Tody. B. Detailed spectrogram (left) and power spectra (right) of the train marked in A with an asterisk.
with Kepler (1977), suggested the *Todus* group is monophyletic and developed prior to the Pleistocene. Thus, the opportunity existed for Pleistocene sea-level changes to have created the conditions needed for the variation in vocalizations that we observed.

We cannot dismiss the possibility that more recent habitat fragmentation is the cause of the

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**TABLE 2.** Discriminant function analysis, using a cross validated method, testing for geographic variation in the characteristic song of the Cuban Tody. IJ: Isla de la Juventud; PR: Pinar del Río; Mt: Matanzas; CA: Ciego de Ávila; Cm: Camagüey; SC: Santiago de Cuba; Gt: Guantánamo.

<table>
<thead>
<tr>
<th>Classified as</th>
<th>IJ</th>
<th>PR</th>
<th>Mt</th>
<th>CA</th>
<th>Cm</th>
<th>SC</th>
<th>Gt</th>
</tr>
</thead>
<tbody>
<tr>
<td>IJ</td>
<td>20</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PR</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Mt</td>
<td>1</td>
<td>2</td>
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<td>0</td>
<td>0</td>
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<td>1</td>
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<td>Cm</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>SC</td>
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<td>4</td>
<td>8</td>
<td>3</td>
<td>7</td>
<td>45</td>
</tr>
<tr>
<td>Gt</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>8</td>
<td>3</td>
<td>8</td>
<td>50</td>
</tr>
<tr>
<td>Total n</td>
<td>24</td>
<td>13</td>
<td>9</td>
<td>9</td>
<td>3</td>
<td>8</td>
<td>50</td>
</tr>
<tr>
<td>% correct identification</td>
<td>83.3</td>
<td>38.5</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>12.5</td>
<td>90.0</td>
</tr>
</tbody>
</table>
observed variation in the Cuban Tody songs, as proposed for the Rufous-collared Sparrow (Zonotrichia capensis) by Tubaro et al. (1993). Pleistocene glaciation is believed to have influenced the present distribution of many Antillean taxa, but the paucity of information regarding the differentiation of these taxa has left uncertain how much these ancient climatic fluctuations contributed to the speciation process (Pregill and Olson 1981). Further, for the last 8,000 years, after the early Holocene subsidence of seas levels (Iturralde-Vinent 2004), Cuba has been a single continuous island through which todies could potentially move with relative ease. The potential for genetic flow was interrupted again in the last five centuries through ongoing deforestation (Fig. 1).

Distinguishing between the impacts of ancient and recent isolation of tody populations requires further research. Regardless of the cause of vocal differentiation, we suggest that more detailed studies are needed to explore the extent to which the todies’ two vocally-distinct populations represent “incipient species” on Cuba. We believe that it would be important to investigate the functions of song in Cuban Todies; whether singing is entirely for mate attraction or serves both for mate attraction and territorial defense (Payne 1979; Gibson 1989; Westcott 1992, 1997), or even whether the song serves as a contact communication in mixed-species flocks (Catchpole and Slater 1995), in which we have also observed singing by Cuban Todies. We believe studies of additional species of birds, looking for consistent geographic patterns in vocal differentiation, will also have a role in helping us understand the evolution of tody vocalizations, and more generally in understanding the evolutionary history of the Cuban avifauna.

TABLE 3. Standardized canonical discriminant function coefficients for Cuban Tody songs.

<table>
<thead>
<tr>
<th>Function</th>
<th>Parameter</th>
<th>I</th>
<th>II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interval between notes</td>
<td>0.801</td>
<td>0.314</td>
<td></td>
</tr>
<tr>
<td>Note duration</td>
<td>0.100</td>
<td>0.039</td>
<td></td>
</tr>
<tr>
<td>Number of notes</td>
<td>0.561</td>
<td>-0.930</td>
<td></td>
</tr>
<tr>
<td>Peak frequency</td>
<td>-0.098</td>
<td>0.557</td>
<td></td>
</tr>
<tr>
<td>Interval between songs</td>
<td>0.248</td>
<td>0.643</td>
<td></td>
</tr>
<tr>
<td>Initial frequency</td>
<td>0.065</td>
<td>0.377</td>
<td></td>
</tr>
<tr>
<td>Final frequency</td>
<td>-0.204</td>
<td>-0.018</td>
<td></td>
</tr>
</tbody>
</table>

ACKNOWLEDGMENTS

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lidae); the Mynootherida sarinamensis complex. Auk 116: 83-96.


OBSERVATIONS ON THE NATURAL HISTORY OF THE ROYAL SUNANGEL (HELIANGELUS REGALIS) IN THE NANGARITZA VALLEY, ECUADOR

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ABSTRACT.—The Royal Sunangel (Heliangelus regalis) is endemic to sandstone ridges in southeast Ecuador and northeast Peru. This hummingbird is currently considered endangered, although little has been published on its natural history, distribution, and conservation. We found H. regalis in three habitat types, but abundance was higher in stunted shrubland, at ridgetops. It was observed to feed on seven plant species, mostly following regular feeding routes, between 0 and 2.5 m above ground. We describe six different vocalizations, as well as two flight displays, and observations on social interactions. We also discuss its current conservation status in Ecuador, where we estimate that ~2,500 individuals might persist. Received 5 April 2010. Accepted 8 September 2010.

We undertook observations on the natural history of H. regalis at two different localities (above Miazi and above Yankuam) during field work for a rapid assessment of two sandstone, flat-top ridgetops (locally called “tepusis” because of resemblance to the Guianan table-top mountains) currently protected by the local community of Las Orquideas (04° 13’ 58.8” S, 78° 39’ 0” W, 900 m asl). We present our field observations to briefly assess its habitat preferences, comparing our results with previous habitat descriptions (Fitzpatrick et al. 1979, Seddon et al. 1996), contribute data on its diet, displays, vocalizations, and social interactions, and discuss its current conservation status.

OBSERVATIONS

Field Identification.—Field identification of males was straightforward, as H. regalis is the only hummingbird entirely violet-blue, which looks mostly black in poor light conditions. Males were identified by pale tawny underparts with some green streaking-spotting in the throat and a plain tawny buff crescent in the chest with a rather long, deep blue forked tail (Schulenberg et al. 2007). There was no overlap with other Heliangelus species and identification of female plumage birds is considered accurate (Krabbe and Ahlman 2009).

Habitat.—We observed H. regalis in three different vegetation types (Table 1). On 8 April 2009, we observed a single female in the under-story of stunted shrubland on a ridgetop above Miazi (04° 15’ 0” S, 78° 37’ 1.2” W; Fig. 1). Vegetation at this site was characterized by low stature, twisted canopy (2–8 m in height), many epiphytes and hemiepiphytes, and dense under-
TABLE 1. Habitat types where H. regalis was recorded in two localities in the Nangaritza Valley, Zamora Chinchipe Province, southeast Ecuador.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Above Miazi</th>
<th>Above Yankuam</th>
<th>Elevation (m asl)</th>
<th>Terrain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dense foothill forest</td>
<td>1 female/1 male</td>
<td>1,250/1,300</td>
<td>Slopes</td>
<td></td>
</tr>
<tr>
<td>Dense lower montane forest</td>
<td>1 female/2 males</td>
<td>1,550–1,650</td>
<td>Slopes</td>
<td></td>
</tr>
<tr>
<td>Stunted shrubland and paramo-like habitat</td>
<td>1 female</td>
<td>1 female/4 males</td>
<td>1,300 at Miazi, 1,800–1,850 at Yankuam</td>
<td>Ridgetop</td>
</tr>
</tbody>
</table>

story. This was the only individual observed despite considerable mist-netting and point-count sampling at this locality.

A female was mist-netted at 1,250 m elevation on the slopes of a sandstone mountain above Yankuam Lodge (04° 15' 7.2" S, 78° 40' 1.2" W) on 15 April 2009, and a male was observed feeding at mid-strata in dense foothill forest characterized by 15–25 m canopy height, and dominated by several species of Rubiaceae, Euphorbiaceae, Melastomataceae, Myrsinaceae, Clusiaceae, Meliaceae, and Podocarpaceae with...
scattered Dictiocaryum lamarckianum, Iriartea spp., and Wettinia spp. palms. Two separate males and a single female were observed on 17 April 2009 in dense lower montane forest above Yankuam (Table 1). This forest type was characterized by a fairly discontinuous canopy with an average height of 10 m (max = 12 m) with lower vegetation where limestone was exposed. Dominant families were Euphorbiaceae, Clusiaceae, Cunoniaceae, Rubiaceae, Humiriaceae, and Ericaceae. The understory was dense (~ 80% ground cover in some areas) including patches of ground bromeliads with heavy loads of mosses, vine tangles, and epiphytes. Of the observed individuals, one male and one female were in a natural forest gap, while another male was in dense and tangled understory feeding at edges of trails, where vegetation was sparser than in areas away from trails.

At least four males and one female were observed feeding at shrubby edges and in tangled interior on the ridgetop of the sandstone mountain above Yankuam (Table 1) on 17 and 19–20 April 2009; three males were observed performing aerial displays near a tall rocky outcrop at the edge of the forest. Two distinctive but intermixed habitats occurred in this area: (1) stunted shrubland, and (2) an atypical paramo-like vegetation, despite the low altitude for paramos (Sierra 1999). These habitats were characterized by trees and bushes of low stature, a canopy at 2–8 m in height with ‘emergent’ trees barely exceeding 5 m. The understory was dense, reaching 75–80% cover in some areas; the ground cover was also dense with many ground bromeliads, acaulescent rosettes (those having or appearing to have no stem), paramo-like herbs, and terrestrial mosses. The density of epiphytes and mosses was low, but typical paramo families and genera were dominant, including Macleania and Cavendishia (Ericaceae), Macrocarpaea (Gentianaceae), Meriania and Miconia (Melastomataceae) bushes, ground Asteraceae, and Wienmania (Cunoniaceae).

Vegetation types described correspond to previous ecosystem classifications for the Nangarita area. Detailed information about general vegetation types in the Nangarita Valley is provided by Foster and Beltrán (1997), Palacios (1997), Neill (2007), and Jadan (2010).

Feeding Behavior.—A male H. regalis was feeding in dense foothill forest by hovering at an epiphytic Guzmania (Bromeliaceae) bromeliad ~3 m above ground. At least one other male fed by hovering at several flowers of two ground bromeliads Tillandsia cf. asplundii, and one ericad shrub Disterigna alaternoides, both with fairly long (~ 2 cm) corollas, in dense lower montane forest. Feeding heights ranged from 0.30 to 2.5 m.

We observed 34 feeding visits of H. regalis to seven different plant species in stunted shrubland and paramo-like habitat above 1,800 m. Plants used for foraging included a small terrestrial yellow-flowered Guzmania gracilior (Bromeliaceae) with six feeding visits; a larger, green-and-pink-flowered epiphytic G. garciaensis (4 feeding visits); the epiphytic, fuchsia-flowered Elleanthus ampliflorus (Orchidaceae) (1 visit); an unidentified small epiphytic bromeliad (1 visit); the stunted tree Macrocarpaea harlingii (Gentianaceae) was visited nine times; an epiphytic Cavendishia spp. and a shrub Macleania spp. (both pink-flowered Ericaceae) were visited six and three times, respectively. Feeding heights ranged from 0 to 2.5 m.

H. regalis fed by hovering on most feeding visits (94%, n = 34), but perched on a nearby twig at three of 10 flowers probed during a single visit to a ground-living small bromeliad. It perched on the ground at one of five flowers probed during another visit to a ground bromeliad. A single male was observed to return to the same flowering plants at 8–15 min intervals, following a somewhat similar route. It first visited a 3-m tall Macrocarpaea harlingii where it fed on several individual flowers (but not on the same flowers during consecutive visits), and then moved either to another Macrocarpaea or to an epiphytic Guzmania garciaensis, both ~5 m from the first Macrocarpaea. Subsequently, it visited a cluster of 10 ground G. gracilior, and left the area in the same direction from which it arrived. Another individual male was observed making regular visits to a patch of small G. gracilior and a patch of Macleania spp. shrub, returning to a perch of 2 m height.

Social Interactions.—Few interactions with other hummingbirds were observed. One male H. regalis was observed displacing, but not directly attacking or chasing, a male Ecuadorian Piedtail (Phlogophillus hemilencurus) at feeding sites (in ridgetop shrubland above Yankuam), and a male attacked and chased a male Green-fronted Lancebill (Doryfera ludovicae) when it hovered in front of ericaceous flowers in the same site; minutes later a D. ludovicae returned and hovered
in front of the same flowers without being displaced.

No other aggressive behaviors were reported although other hummingbird species occurred in feeding areas used by *H. regalis*. No interactions were observed in lower elevation forests above Yankuam (below 1,700 m). Intense disputes were observed among Brown Violetears (*Colibri delphiaceae*), Rufous-vented Whitetips (*Urosticte ruficrissa*), Violet-fronted Brilliants (*Heliodoxa leadbeateri*), and Blue-fronted Lancebill (*D. johannae*) at flowering forest trees and epiphytes, but no *H. regalis* was observed in those interactions. The only female found above Miazi was observed displacing an unidentified hummingbird and perching upright, with her neck stretched, possibly in territorial dispute.

**Vocalizations.**—We heard and tape recorded several types of vocalization. A tame and curious male approached one observer (J. F. Freile) and remained perched motionless for 1 min. He uttered a sharp, high-pitched, fast *tchúp tchúp!* before take off with the last note more emphatic. A female in the same area perched in a natural forest gap uttered a thin, high-pitched *tjiup!* We failed to record both vocalizations.

A feeding male uttered an emphatic *tchúp* or *tchúp!* every 3.5–6 sec (deposited at www.xenocanto.org; XC 45910; Fig. 2A), whereas other feeding calls were uttered at shorter intervals (2–2.5 sec), or in short two- to three-notes descending series *tchúp-tchúp* or *tchúp*—with the first note higher (XC 45911; Fig. 2A). The duration of each note was ~0.1 sec for the feeding call (Fig. 2A), while frequency ranged from 1.5–1.8 to 17–19 kHz (call 2A), and 1.5 to 21 kHz (call 2A).

Two displaying males produced a fast chattered series of very high *tEEp* or *jéét* notes lasting 2.5–4.5 sec (XC 45912; Fig. 2B). This vocalization contained 19 notes of 0.10–sec mean duration (0.07–0.15 sec) with frequencies ranging from 1.7 to 16.69 kHz. Two males were observed in stunted shrubland and heard in intense dispute, constantly vocalizing an endless, thin, high-pitched jumble *tjiijèt'tjiijèt'tjiijèt'tjiijèt*... notes uttered at a much faster rate than regular vocalizations. This dispute and chatter was only interrupted when a third male dashed towards them. Our recordings are uploaded to www.xenocanto.org (XC 45910–45915) as only a single recording of *H. regalis* is currently deposited in a public audio library (Macaulay Library 18046; N. Krabbe, pers. comm.).

**Display Flight.**—Three males were observed performing display flights in ridgetop stunted shrubland, one above a nectar source (*Macrocarpaea harlingii*) and two above a shrub edge and rocky outcrop. In display, one male ascended ~5 m in vertical flight, described one oval, possibly two, at the highest point and descended describing a semicircle to the same perch; the second male followed the first's display flight constantly vocalizing (Fig. 3A). A somewhat similar display was also observed with a male ascending 10–12 m and then descending in a semicircle, and diving out of sight (Fig. 3B).

**DISCUSSION**

*Helianthus regalis* is generally regarded as locally fairly common (Seddon et al. 1996; Schulerberg et al. 2001, 2007; Dauphiné et al. 2008). Schulerberg et al. (2001) suggested the Cordillera Azul might represent the center of abundance of *H. regalis*, and that it might be less threatened than currently believed. However, with a global range of only 2,100 km², its global population has been roughly estimated at 2,500–9,999 individuals (BirdLife International 2009).

Our observations suggest the abundance of *H. regalis* can vary across different vegetation types. However, in accordance to previous reports (Fitzpatrick et al. 1979, Davis 1986, Seddon et al. 1996, Dauphiné et al. 2008), stunted shrubland appears as its preferred habitat, at least judging from relative abundances at the three vegetation types surveyed in this study. Higher numbers in stunted shrubland and paramo-like vegetation suggest these habitats provided plentiful food resources during the study season. Low detection in dense lower montane and foothill forests might also account for lower numbers in these forests (Poulsen et al. 1997). We cannot rule out seasonal movements along vegetation gradients as previously suggested by Seddon et al. (1996). Habitat suitability appears to be higher for stunted shrubland, but defining optimal habitats solely based on relative abundance has proven to be misleading (van Horne 1983, Morris 1987).

*H. regalis* in stunted shrubland likely fed on most available nectar sources. Flowering was limited to a few individual plants of a few species. Our data suggest that *H. regalis* was not strongly dependent on one food plant species as found in the type locality, where the species was reported as highly dependent on *Brachyotum quinquenerve* (Melastomataceae) (Fitzpatrick et al. 1979); it
should be noted that \textit{B. quinquinerve} was absent from our study area. Dauphiné et al. (2008) also reported few food plants, but failed to identify them to the species level and provided no information on flowering at their study site. Males and females, as previous authors (Seddon et al. 1996, Dauphiné et al. 2008) have suggested, might feed at different elevations or different food plants; a suggestion we failed to prove as we observed few females.
Fitzpatrick et al. (1979) and Seddon et al. (1996) reported perching to be a more common foraging method than hovering, in contrast to our observations. We suggest these discrepancies indicate local or seasonal differences in feeding strategies, considering that Seddon et al. (1996) performed more prolonged observations (45 observations of males, 44 of females).

Observations were limited to 6 hrs in stunted shrubland and 'paramo', but we suspect _H. regalis_ followed regular feeding routes in fairly regular time periods within a fixed territory. Two events of territorial defense were observed which, in accordance to previous observations (Fitzpatrick et al. 1979, Seddon et al. 1996), suggest territoriality (Feinsinger and Colwell 1978). Other _Heliangelus_ species are also reported to be territorial (Ortiz-Crespo 2003).

Vocalizations are generally similar to those previously described (Schulenberg et al. 2007), but displaying notes were uttered in fast chattered series, contrary to the high _teep_ note described by Schulenberg et al. (2007). The dispute calls we report are similar to a series of _tick_ notes described by Fitzpatrick et al. (1979) in male-male chases. To our ears, they appear harsher, more metallic, and more chattered than those described by Fitzpatrick et al. (1979).

Displays differed from those observed at the type locality (Fitzpatrick et al. 1979) as we did not observe birds repeating the circular flight towards the opposite side of perches in a figure-8 pattern. More detailed observations are needed to elucidate if display flights differ locally.

_H. regalis_ is apparently fairly numerous in stunted ridgetop shrubland and paramo-like habitats at Las Orquídeas sandstone ridges. At least five different birds were found (one female, four males) in a small sampled area at the ridgetop (~ 0.02 km$^2$; i.e., 500-m linear transect with a 40-m width band), suggesting a healthy population. These observations provide a rough estimate of 250 individuals/km$^2$ in the stunted ridgetop shrubland habitat that _H. regalis_ seemingly preferred during our study. An estimate of the area covered by this forest type (Fig. 1) resulted in 10.11 km$^2$ of the habitat where _H. regalis_ was most abundant in the Nangaritza Valley. This
suggests the total population in the Ecuadorian portion of *H. regalis* range might total ~2,500 individuals. These numbers are crude as better population size estimates and trends are needed.

*H. regalis* is seemingly less numerous in lower elevation montane and foothill forests above Yankuam Lodge. Only three males and one female were observed during 7 days of point-count surveys above Yankuam, in dense foothill and dense lower montane forests, despite a total of 25 10-min point counts. *H. regalis* was not found in similar habitats above Miazi during 21 10-min point counts, but one female was observed by random sampling on a small ridgetop. We sampled ~2–3 km between both study sites. This might indicate 1–1.5 birds/km in these two forest types, but dense habitat might reduce detection.

**CONSERVATION IMPLICATIONS**

Habitat loss is still incipient along the Ecuadorian range of the species, but mining concessions represent a serious forthcoming threat to the endemic biodiversity of the Cordillera del Cóndor. There is major interest by the Ecuadorian government to consolidate mining extraction in the Cordillera del Cóndor region because of apparently large deposits of gold and copper, as well as silver, silica, and other minerals and metals (Lopez et al. 2003, Fontbote et al. 2004, Neill 2007, Drobe et al. 2008; see also www.aurelianecuador.com; www.corriente.com; www.kinross.com). Currently, several areas north of Nangaritza Valley are being prospected by mining companies, and access roads are being rapidly opened and improved. Populations of species confined to these poor-soil growing forests are imminently threatened as large sandstone ridges will potentially be opened to large-scale mining. Under this scenario, we consider accurate the status of globally Endangered (BirdLife International 2009) for *H. regalis* despite current population figures suggesting it is less threatened.

Conservation initiatives are underway in the Nangaritza Valley, including private birdwatching tour operators, land protection, and an ongoing management plan developed by Fundación Arco Iris of Loja along with local communities. These initiatives benefit from biodiversity surveys that support the biological and hydrological importance of the Nangaritza Valley. We encourage others to undertake more specific studies in the region, particularly to assess populations and habitat of globally threatened species including *H. regalis*. Easy access to the Nangaritza sandstone ridges facilitate biological surveys and bird studies of an avifauna generally regarded as difficult to reach.

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NESTING BEHAVIOR OF SZECHENYI'S MONAL-PARTRIDGE IN TREELINE HABITATS, PAMULING MOUNTAINS, CHINA

KAI ZHANG,1 NAN YANG,1 YU XU,1 JIANGHONG RAN,1,3 HUW LLOYD,2 AND BISONG YUE1

ABSTRACT—We report nesting behavior of Szechenyi's Monal-Partridge (Tetraophasis szechenyii) in treeline habitats of the Pamuling Mountains, Sichuan Province, China. Szechenyi's Monal-Partridge used both ground and tree nests. Ground nests were scrapes in the soil, positioned at the base of a tree or scrub, and occurred in all habitats except Sichuan kobresia (Kobresia setchwanensis) meadow. Tree nests were cup shaped and placed 1.9–12.0 m above ground level, distributed proportionally in all habitats except scrub hollyleaf-like oak (Quercus aquifolioides) and Sichuan kobresia meadow habitats. The proportion of nest types between first and re-nesting attempts did not vary significantly. Only 54% of ground nests and 33% of tree nests survived until hatching with predation being the principal cause of ground nest failure. Hatching success was 97%. We recorded six re-nesting attempts, four of which were tree nests, but all were unsuccessful. Preserving a mosaic of treeline habitats that include ground vegetation, and fir/oak woodland habitat will be essential for maintaining suitable nesting habitats for Szechenyi's Monal-Partridge in the Pamuling Mountains. Received 4 March 2010. Accepted 14 August 2010.

Most Galliformes are typically ground-nesting species. Two exceptions to this general rule have been discovered among Tragopan and Tetraophasis (Li 1996). Species of Tragopan typically nest above the ground in trees (Johnsgard 1999, Deng et al. 2005), whereby members of Tetraophasis use two types of nests, either on the ground or at some height in trees (Lu and Lu 1991, Wu et al. 1994). Few data exist regarding many aspects of the breeding ecology of members of the genus Tetraophasis (Lu and Lu 1991, Potapov 2002, Yang et al. 2009). This genus is endemic to China and consists of two species: Verreaux’s Monal-Partridge (T. obscurus), which is largely restricted to rhododendron (Rhododendron spp.) scrub and alpine meadows in western China, and Szechenyi’s Monal-Partridge (T. szechenyii) which occurs in a number of montane habitats in southwestern China, including fir (Abies spp.) forests, rhododendron scrub, and alpine meadows (MacKinnon and Phillipps 2000). We describe the nesting behavior of Szechenyi’s Montal-Partridge in treeline habitats of the Pamuling Mountains, Sichuan Province, China.

METHODS

Study Area.—Our study was conducted over a 4-year period in the Pamuling Mountains (30° 06′ N, 101° 11′ E), Yajiang County, Ganzi Tibetan Autonomous Prefecture, Sichuan Province, China. The study area ranges in elevation from 3,900 to 4,200 m and is dominated by a variety of different habitat types. The most dominant habitat type is hollyleaf-like oak (Quercus aquifolioides) forest (covering ~50% of the study area), distributed along the southern-most slopes of the region. This forest eventually grades into scrub along the western slopes, accounting for 9% of the study area. Flaky fir (Abies squamata) and Masters larch (Larix mastersiana) coniferous forest (covering 39% of the study area) is the second most widespread habitat. Violet-purple rhododendron (Rhododendron nitidulum) scrub (covering 11% of the study area) is the third most widespread habitat, while Sichuan kobresia (Kobresia setchwanensis) meadow makes up a smaller proportion (~1%) of the Pamuling Mountains treeline habitats (Xu et al. 2008).

Nest Surveys.—We searched for nests from April to June 2006, between March and May in 2007 and 2008, August 2008, and also between March and June 2009. Nests were found by locating nesting birds (n = 8) previously captured by drop-netting and fitted with radio transmitters (19-g necklace-type, Holohil Systems Ltd., Carp, ON, Canada), and by systematically searching suitable areas of habitats. Each nest was checked regularly at intervals of 1–2 days. Each covey (consisting of a mixed group of 1 adult breeding pair, up to 3 helpers of either gender and a single brood) from all located nests was observed after incubation to assess chick survival and to monitor any subsequent nesting attempt. Nests discovered either early in the breeding season or in the middle of the season with ≥ three eggs were categorized as...
first nests, whereas those found with < three eggs, or nests found late in the season were categorized as re-nesting attempts (Yang et al. 2009; KZ, unpubl. data). We recorded the following variables for each nest: breeding group composition (breeding pairs and helpers), nesting attempt, nest type (either ground or tree nest), nest characteristics (structure and material), nest contents, nest tree (scrub) species, and habitat characteristics (habitat type, canopy cover, and scrub cover). Canopy cover and scrub cover were measured within a 10-m diameter plot around each nest.

Statistical Analyses.—Analyses were conducted using SPSS Version 13.0 (SPSS Institute 2004). We included only the first nesting attempt by each female in the subsequent analyses to avoid pseudo-replication, and analyzed the few re-nesting attempts separately. Chi-square test of independence was used to compare the proportion of nest types between nesting attempts. Data corresponding to re-nesting attempts were excluded from the analysis. We also used Chi-square Goodness of Fit tests to examine tree nest site preferences among habitat types. Mann-Whitney U-tests were used to detect differences between ground and tree nests. Statistical tests were two-tailed and \( P < 0.05 \) was interpreted as being statistically significant. Mean ± SD values are presented. We combined all egg measurement data from ground and tree nests as they did not differ (\( Z = -1.824, P = 0.068; Z = -1.178, P = 0.24 \), for egg length and width, respectively).

RESULTS

Nest Surveys.—Sixty-eight breeding groups were detected over the four consecutive breeding seasons (18 in 2006, 16 in 2007, 17 in 2008, and 17 in 2009). Szechenyi’s Monal-Partridge in the Pamuling Mountains treeline habitats constructed nests either on the ground or in trees. Fifteen ground nests (all active; 68% of total active nests) and 63 tree nests (56 used and 7 active; 32% of total active nests) were found during the study period. Thirteen ground nests were first nests and two were re-nesting attempts. Three active tree nests were first nests while the remaining four were classified as re-nesting attempts. No third nesting attempts were identified. Tree nests were more common in re-nesting attempts than in first nests (50 and 17%, respectively), but the difference was not significant (Fisher’s exact test, \( P = 0.40 \)).

Nest Characteristics and Nest-site Selection.—Ground nests (\( n = 15 \)) were scrapes in the soil and lined with leaves, sticks, and bark, usually positioned at the base of a tree or scrub (Fig. 1A). They occurred in all habitats except Sichuan kobresia meadow, and had lower canopy vegetation cover (13 ± 14%, range = 0-40%, \( n = 13 \)) when compared with tree nest sites (30 ± 17%, range = 20-50%, \( n = 3 \)); this difference was not significant (\( Z = -1.835, P = 0.066 \)). Tree nests (\( n = 63 \)) were cup shaped (Fig. 1B) and constructed of moss, lichen, and feathers although some nests also contained fragments of man-made cloth. They were positioned 1.9-12.0 m above ground level either at the base of the tree branches and adjacent to the main trunk in coniferous forest and rhododendron scrub, or at the top of trees in oak forest. Tree species used included Abies squamata (61%), Quercus aquifolioides (31%), and Larix potaninii (8%). No tree nests were found within either the scrub holly-leaf-like oak habitat or Sichuan kobresia meadow; they were distributed proportionally among the three remaining habitat types (\( \chi^2 = 0.194, df = 2, P = 0.91, n = 56 \)).

Eggs and Nesting Success.—Eggs (\( n = 46 \)) were pinkish brown with fine, well-dispersed burgundy-colored spots, and measured 53.8 ± 2.6 mm (range = 47-59 mm) \( \times 37.4 ± 1.9 \) mm (range = 33-42 mm). Only 54% (\( n = 7 \)) of ground nests survived until hatching, compared with 33% (\( n = 1 \)) of tree nests. The principal cause of ground nest failure was predation which accounted for 50% of all failed nests, while severe weather conditions (33%), and human disturbance (17%) accounted for the remaining nest failures. Hatching success was 97% (\( n = 31 \) eggs from 8 nests). Twelve chicks (\( n = 27 \) from 7 ground nests) survived to fledge, while three chicks from the one tree nest failed to survive.

Changes in Nest Location and Nest Type.—We documented re-nesting attempts on six occasions during the 4-year period. There were two occasions where only re-nests were detected: one was a ground nest in 2008, and the other was a tree nest in 2009. We documented the nest location and nest type for both nesting attempts on the other four occasions. On two occasions (once each in 2008 and 2009), females re-nested in the same nest types. One female reused the tree nest after the chicks from first nest failed to survive. the other female changed ground nest location in a re-nesting attempt following nest predation. Females switched nest locations and nest types from ground to tree nests on the other two occasions (once each in 2007 and 2009) following...
failure of first nests due to extreme weather conditions. One female abandoned a ground nest in violet-purple rhododendron scrub and built a new nest in flaky fir forest, ~190 m from the original nest. The other female abandoned a ground nest in hollyleaf-like oak forest and used a tree nest in the same habitat from a previous season, ~300 m from the original nest. Both re-nests were also unsuccessful because of predation (either by corvids or mammals).

DISCUSSION

Elevated nests have been reported for several species of Galliformes, e.g., Green Junglefowl (Gallus varius), Salvadori's Pheasant (Lophura momota), Ring-necked Pheasant (Phasianus colchicus), Palawan Peacock-Pheasant (Polyplectron na‐poleon), Congo Peacock (Afropavo congensis), and Mikado Pheasant (Syrmaticus mikado) (Johnsgard 1999). The elevated nest is a variation rather than a distinct shift from the ground nest. Two female Szechenyi's Monal-Partridges in the Pamuling Mountains changed nest locations and nest types from the ground to tree nests. Similar tree nest observations have been noted with Cabot’s Tragopan (Tragopan cabotti) but, unlike this species, all arboreal tree nesting by Szechenyi’s Monal-Partridge did not rely on use of pre-existing nest structures for nest construction, such as natural platforms or nests from other species or taxa (Deng et al. 2005), but included collection of new nesting material for the construction of a completely new nest.

Most Szechenyi's Monal-Partridges in the Pamuling Mountains were ground nesting, but some also nested in trees. The tree nest use pattern by Szechenyi’s Monal-Partridge reflected the proportion of available treeline habitat types in the region. We would expect ground nesting would be more
common in low-lying violet-purple rhododendron scrub and scrub hollyleaf-like oak habitat, as few tall trees are available in these habitat types. Tree nests were not as successful as expected in our study, probably due to small sample sizes.

Re-nesting attempts and changes in nest locations or habitats between nesting attempts following nest failure have been documented for several species of Galliformes including Willow Ptarmigan (*Lagopus lagopus*) (Parker 1981), Wild Turkey (*Meleagris gallopavo*) (Badyaev et al. 1996), Black Grouse (*Lyrurus tetrix*) (Marjakangas et al. 1997), and Chukar (*Alectoris chukar*) (Lindbloom et al. 2003). Re-nesting in Galliformes was initially thought to be rare (Patterson 1952), but research has shown that re-nesting rates can exceed 40% for some species (e.g., Petersen 1980, Bergerud 1988). Changes in nest locations following nest predation might be a response to avoid revisiting by the predator (O’Reilly and Hannon 1989, Marjakangas et al. 1997). We suspect that unpredictable and severe weather conditions in our study may also be involved. Further systematic nest studies with large sample sizes are needed to identify the relationship between the probability of changing to a different nest location or nest type and causes of previous nest failure. The benefits of switching nest location and nest type for Szechenyi’s Monal Partridge remain unknown as our sample sizes were too small and all re-nesting attempts also failed. What is apparent from our observations however is the importance of preserving a mosaic of treeline habitats that include ground vegetation, and fir/oak woodland habitat to maintain suitable nesting habitats for the Szechenyi’s Monal Partridge in the Pamuling Mountains.

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LITERATURE CITED


REPRODUCTIVE STATUS OF SWALLOW-TAILED KITES IN EAST-CENTRAL ARKANSAS

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ABSTRACT.—The Swallow-tailed Kite (Elanoides forficatus) formerly bred in Arkansas, but no nesting attempts were observed in the state for over a century. We initiated a study in 2001 to investigate the species’ reproductive status in east-central Arkansas, USA. We located five nests between 2001 and 2009, all of which failed. Two nests were abandoned (one due to researcher caused disturbance), one failure was likely caused by a Red-shouldered Hawk (Buteo lineatus) or Barred Owl (Strix varia), one was suspected to be caused by a rat snake (Elaphe obsolete), and one failed from unknown causes. Nests were built in overcup (Quercus lyrata) and Nuttall oaks (Q. texana) with a mean (± SD) diameter at breast height of 83.92 ± 7.20 cm, mean tree height of 31.28 ± 4.78 m, and mean projection of 7.15 ± 5.66 m above surrounding trees. Nests were at a mean height of 25.09 ± 4.85 m and positioned 0.30 ± 2.36 m above the surrounding trees. All nests were within a circular area 4 km in diameter. Our discovery of a nest in 2002 represented the first documented case of nesting Swallow-tailed Kites in Arkansas in >100 years and is a considerable (370 km) distance from the closest known nesting site in Louisiana. Received 3 May 2010. Accepted 11 October 2010.

The Swallow-tailed Kite (Elanoides forficatus) formerly bred in at least 16 states from Florida and the Southeast Coastal Plain west to central Texas and north through the Mississippi and Ohio river drainages to Minnesota (Meyer and Collopy 1995). The population experienced a drastic reduction in numbers around the turn of the 19th century (Cely 1979) and now breeds in portions of only seven southeastern states (Meyer 2004a). Loss of suitable habitat following destruction of bottomland hardwood forests (Twedt and Loesch 1999), agricultural development, and shooting were likely the primary reasons for the widespread decline (Cely 1979, Meyer 1995, Meyer and Collopy 1995). Observations of Swallow-tailed Kites increased in former breeding areas in the 1940s (Cely 1979), suggesting small scale reoccupation of historical range (Brown et al. 1997). However, reasons for this kite’s inability to fully reoccupy its former range mostly remain unknown (Meyer and Collopy 1995).

Swallow-tailed Kites were considered relatively abundant in Arkansas lowlands at the end of the 19th century, but became rare by 1910 with the last known nesting attempt occurring in 1890 (Howell 1911). A sighting of a single kite occurred in northwest Arkansas in October 1913 (Smith 1915), and from 1915 to 1986, only two secondhand accounts of kites were reported; one in 1935 and a pair of kites observed on 10 July 1949 (Baerg 1951). A subsequent lack of reports suggests the species may have been extirpated from Arkansas in the late 1940s (James and Neal 1986). Four sporadic observations of Swallow-tailed Kites during migration occurred between 1986 and 1997, but it was not until 1998 that a pair was observed during the breeding season. Observations in 1998 occurred in the White River National Wildlife Refuge (WRNWR) and, based on these reports, we initiated a study to investigate the breeding status of Swallow-tailed Kites in the refuge. Our objectives were to: (1) document Swallow-tailed Kites present during the breeding season in the White River National Wildlife Refuge and (2) locate, monitor, and record nesting attempts.

METHODS

Study Area.—The White River National Wildlife Refuge, in east-central Arkansas (34° 22' N to 34° 39' N, 90° 59' W to 91° 22' W) comprises ~64,700 ha and is one of the largest remnants of contiguous bottomland hardwood forest in the Mississippi Alluvial Valley. It consists primarily of bottomland hardwood forest with small sections of upland hardwood forest, scattered fallow and agricultural fields, 356 natural and man-made lakes, >140 km of the White River, and a large number of bayous and sloughs. Dominant tree species include overcup oak (Quercus lyrata),...
TABLE 1. Dates of observation and nest discovery, and nest fates of Swallow-tailed Kites in the White River National Wildlife Refuge, Arkansas, USA.

<table>
<thead>
<tr>
<th>Year</th>
<th>Obs</th>
<th>Observed</th>
<th>Nest found</th>
<th>Stage</th>
<th>Date failed</th>
<th>Stage</th>
<th>Failure cause</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>13</td>
<td>1 May-24 May</td>
<td>24 May</td>
<td>Building</td>
<td>27 May</td>
<td>Building</td>
<td>Abandoned</td>
</tr>
<tr>
<td>2003</td>
<td>7</td>
<td>12 May-24 Jun</td>
<td>23 May</td>
<td>Nestling</td>
<td>27 May</td>
<td>Incubation</td>
<td>Unknown</td>
</tr>
<tr>
<td>2004</td>
<td>17</td>
<td>24 Apr-13 Jul</td>
<td>19 May</td>
<td>Building</td>
<td>28 May</td>
<td>Nestling</td>
<td>Raptor</td>
</tr>
<tr>
<td>2005</td>
<td>12</td>
<td>8 May-21 Jul</td>
<td>23 May</td>
<td>Nestling</td>
<td>30 Apr</td>
<td>Incubation</td>
<td>Possibly ratsnake</td>
</tr>
<tr>
<td>2006</td>
<td>11</td>
<td>17 Apr-3 Jun</td>
<td>17 Apr</td>
<td>Building</td>
<td>26 May</td>
<td>Nestling</td>
<td>Researcher disturbance</td>
</tr>
<tr>
<td>2007</td>
<td>9</td>
<td>24 Apr-8 Jun</td>
<td>15 Apr</td>
<td>Building</td>
<td>26 May</td>
<td>Nestling</td>
<td>Researcher disturbance</td>
</tr>
</tbody>
</table>

* Number of observations involving ≥1 kite.
* Inclusive dates for all kite observations.
* Failure date was estimated as the middle of visitation intervals (2008 failure date known by reviewing video).

Field Procedures.—We searched for kites from early April through mid-July 2001 to 2009. Searches in 2001 and 2002 were based on reported observations and suitable habitat, and were broader than later searches, covering several large areas of the refuge and bordering lands (St. Pierre 2006). Searches in subsequent years focused on areas of previous nests and observations. We conducted searches from a helicopter in 2002 and 2007 following repeated observations of a pair of kites in a localized area. We checked status and stages of nests by monitoring them every 3 to 7 days using binoculars and a spotting scope at 50-100 m from the nest tree. Nests were considered occupied if a kite was on the nest during >1 nest check and we estimated nesting stage by monitoring adult behavior.

We attached snake excluder devices (SNED) (Neal et al. 1998) to trunks of nest trees (none attached in 2002) ≥1 week after incubation began. SNEDs consisted of a thin sheet of aluminum flashing 90 cm high, camouflaged with paint, attached using staples or screws, and greased as an added preventive measure. We used a specially-designed infrared video recording system from Fuhrman Diversified Inc. (Fieldcam: Field Television System: LDTLV/Box/Versacam/IR60, Seabrook, TX, USA) in 2008 near a nest when we estimated nestlings to be 7 days of age. We deployed the camera shortly after sunrise to prevent chicks from being exposed to mid-day temperatures. The camera (dimensions: 30 × 22 × 10 cm) was mounted 3 m from the nest on an adjacent limb within the nest tree and was covered with camouflage fabric.

We noted vegetation characteristics from nest and paired random sites following the BBIRD protocol (Martin et al. 1997, St. Pierre 2006). Random plots were within 250 m of nest trees and were generated using a random number table. Our data collection at nest and random sites included: height of all overstory trees within an 11.3-m radius circular plot, emergence of nest or plot center trees above surrounding trees, diameter at breast height (DBH) of nest and plot center trees, and distance to nearest forest edge. Nest and tree height, DBH, and plot distance from edge were measured using a clinometer, diameter tape measure, and Global Positioning System (GPS) unit, respectively. We used paired t-tests (SAS Institute 2003) for all statistical comparisons except for non-normal data which we analyzed using Wilcoxon’s signed-ranks test. Means ± SD are reported and we considered results significant if $P \leq 0.05$.

RESULTS

We located five nests of Swallow-tailed Kites in the White River National Wildlife Refuge; one each during 2002, 2004, 2005, 2006, and 2008 (Table 1). All nesting attempts failed. We observed no Swallow-tailed Kites in 2001. We observed a single kite in 2003 and a pair in both 2007 and 2009, but were unable to locate a nest during these years; we failed to observe any fledglings in years we did not locate nests. We found the 2002 nest during a helicopter search of an area where we made repeated observations of kites. Upon locating a nest, the helicopter hovered ~50 m from it for <45 sec before leaving the

area. An adult flew from the nest and we observed the nest was completed, but contained no eggs or nestlings. The nest was rechecked several times on a weekly basis from the ground, no adults were present, and we considered it abandoned. We observed an adult on a nest in incubation position in 2004, 6 days after discovering it, but it was unoccupied during the following three nest visits, indicating failure. Nine days after discovering a nest in 2005, we recovered two dead nestlings ~2 weeks of age below the nest tree. Both chicks had wounds on their torsos and wings consistent with the talon spread of a Barred Owl (Strix varia) or Red-shouldered Hawk (Buteo lineatus). We believe failure of the 2006 nest may have been the result of rat snake (Elaphe obsoleta) depredation due to the presence of a long, vertical “track” through grease on the SNED and streaks of grease leading down the trunk onto the ground. We installed a camera in 2008 when we estimated nestlings were 1 week of age. Camera installation took ~2 hrs from the time we arrived below the nest tree to the time we left the nest area. The adult kite remained on the nest until we climbed to within 4 m of it. We checked the nest 2 days later, did not see an adult on it and, after reviewing our video data, discovered the adults did not return following camera installation. We climbed to the nest the following day and recovered two dead nestlings.

All nests and most observations were within a 4-km area (Fig. 1). The 2004, 2005, 2006, and 2008 nests were 3.4 km, 190 m, 270 m, and 1.6 km from the 2002 nest, respectively. Nests were in Nuttall (n = 2) and overcup oaks (n = 3), placed near the tops of trees at a mean (± SD) height of 25.09 ± 4.85 m, and were positioned 0.30 ± 2.36 m above the surrounding canopy. Nest trees had significantly greater DBHs than random trees (Table 2). Nest tree emergence above the surrounding canopy was greater than that of random trees, but not significantly so (Table 2).

DISCUSSION

Our documentation of a Swallow-tailed Kite nest in 2002 represents the first observed nesting attempt in Arkansas in >100 years and is a considerable (370 km) distance from the closest known nesting site in Louisiana (St. Pierre 2006). The individuals we observed were unbanded, but
TABLE 2. Characteristics of Swallow-tailed Kite nest (n = 5) and paired random sites (n = 5) in the White River National Wildlife Refuge, Arkansas, USA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Nest site</th>
<th>Random site</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree height, m</td>
<td>31.28 ± 4.78</td>
<td>27.12 ± 6.40</td>
<td>2.56</td>
<td>4</td>
<td>0.125</td>
</tr>
<tr>
<td>Diameter at breast height, DBH (cm)</td>
<td>83.92 ± 7.20</td>
<td>49.33 ± 15.09</td>
<td>6.74</td>
<td>4</td>
<td>0.003</td>
</tr>
<tr>
<td>Nest tree emergence, m</td>
<td>7.15 ± 5.66</td>
<td>0.42 ± 4.74</td>
<td>3.01</td>
<td>3</td>
<td>0.057</td>
</tr>
<tr>
<td>Distance to nearest edge, m</td>
<td>498.1 ± 56.5</td>
<td>451.9 ± 185.8</td>
<td>0.73</td>
<td>4</td>
<td>0.508</td>
</tr>
</tbody>
</table>

* Wilcoxon's signed-ranks test used for analysis.
* Nest tree emergence data not collected in 2006.

The strong nest site fidelity of the species (Meyer 1995) indicates that reuse of a relatively small area (4 km) for nesting in the refuge suggests at least one individual from the nesting pair observed in 2002 may have returned to nest in subsequent years. The repeated use of this area indicates the existence of suitable nesting habitat. The most important characteristics within the Swallow-tailed Kite’s breeding range are existence of tall, accessible trees and open areas that facilitate prey capture (Meyer 1995). Many relatively tall trees exist throughout the refuge and, although not quantified in this study, the many bayous, sloughs, lakes, and ponds in the refuge likely provide ample openings for prey acquisition. Similar to our results, kites nesting in South Carolina and Florida placed nests near the tops of trees that projected above the surrounding canopy (Cely and Sorrow 1990, Meyer and Collopy 1995, Meyer 2004a). Kites in Arkansas selected nest trees with significantly greater DBHs than those of random trees, which may afford kites stronger nest supporting limbs, decreasing the likelihood of failure during high winds, a common cause of failure in south Florida (Meyer and Collopy 1995, Meyer 2004a).

Cely and Sorrow (1990) noted the variability in tolerance of Swallow-tailed Kites to human disturbances near nests, but indicated most kites appeared unaffected by observer presence early in the nesting cycle. In contrast, the kites we monitored appeared to be sensitive to disturbance near the nest. Helicopters have been used in Florida to search for and monitor kite nests without any negative effects (Meyer and Collopy 1995; Meyer 2004a, b). We cannot discount the possibility that our helicopter search may have caused abandonment in 2002. The pair may have been more prone to disturbance-associated nest abandonment due to the lack of parental investment (i.e., no eggs or young), or the relatively late initiation of the nesting attempt. It is also possible the nest may have been constructed and not used (Meyer 1995) or was depredated during the week following its discovery when no nest checks occurred.

We observed no fledglings despite repeated searches throughout the breeding and post-breeding periods during years when no nests were located. We installed a camera at the nest in 2008 to record nesting activity and causes of failure, because all previously located nests and presumably all undocumented nesting attempts failed. We delayed camera installation until 1 week into the nestling stage to reduce the likelihood of abandonment; the only case of camera-related abandonment was reported by Meyer in Coulson et al. (2008) and occurred during incubation. We believe the camera and not necessarily our climbing to the nest was the reason for abandonment, as we observed two adults flying within 100 m of the nest during camera removal, suggesting they remained in the nest area. We did not monitor the kites’ response to the camera, as we left the area immediately following setup to avoid further disturbing the pair. Had we checked the nest sooner and noticed the kites not returning, we could have removed the system and possibly prevented abandonment. Our experiences, and those reported by Meyer in Coulson et al. (2008) indicate that some nesting Swallow-tailed Kites may be particularly sensitive to disturbances associated with camera systems, especially during incubation and the early nestling stage.

Observations of Swallow-tailed Kites have increased in parts of Arkansas in recent years, which may represent increased visitation by dispersing and migrating kites, or increased effort by observers. Monitoring of kites observed during the breeding season should be undertaken to ascertain if kites are
nesting outside of the White River National Wildlife Refuge, as this is the only area in the state surveyed thoroughly for breeding individuals. In addition, we recommend Arkansas develop a survey and monitoring program similar to that developed in Texas (Shackelford and Simons 2000) to ascertain the species’ status throughout Arkansas.

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NESTLING BEHAVIOR AND PARENTAL CARE OF THE COMMON POTOO (NYCTIBIUS GRISEUS) IN SOUTHEASTERN BRAZIL

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ABSTRACT.—We recorded and quantified the nocturnal activity and parental care of a brooding Common Potoo (Nyctibius griseus) using an infrared camera in southeastern Brazil. Parents alternated care of the nestling and decreased their presence as the nestling grew. Nestling feeding on passing insects while sitting on the nest, movements on the nest, wing exercising, preening, and defecating were recorded primarily while it was alone. The frequency of begging calls per hour was higher when the nestling was accompanied by one of the parents. Nocturnal recordings of this species on the nest revealed behaviors that were not cited in past studies, including: feedings bouts on passing flies performed by the nestling and adults, nestling defecation, and nestling plumage maintenance. The well-known plus newly quantified behaviors of the Common Potoo reinforce their value to survival during the long nestling period. Received 24 May 2010. Accepted 14 September 2010.

Potoos are members of the Nyctibiidae, which is composed of seven species of a single genus (Nyctibius), all geographically restricted to the Neotropics (Cleere 1998, Cohn-Haft 1999, Holyoak 2001). Five species are considered resident in Brazil with the Common Potoo (N. griseus) being the most widespread (Sick 1993) inhabiting rain-forest areas as well as dry forests, cerrado savannas, mangroves, tall secondary growth forests, and partially disturbed areas (Cleere 1998, Cohn-Haft 1999, Holyoak 2001).

Potoos normally assume a motionless posture during the day, perched upright on horizontal branches or on top of a broken branch relying heavily on their cryptic coloration. Shortly before dusk, potoos initiate their nightly activities (Cohn-Haft 1999). Their secretive behavior and cryptic coloration makes them difficult to detect but, once found, detailed observations of their behavior are relatively easy, especially at the nest. Descriptive studies of the nesting behavior of the Common Potoo in neotropical regions have been reported by Goeldi (1896), Muir and Butler (1925), Haverschmidt (1958), Skutch (1970), Tate (1994), Cohn-Haft (1999), Lopes and Anjos (2005), and Corbo and Macarrão (2010).

Published data on the nesting behavior of the Common Potoo were opportunistically obtained by observers during the day or rarely during moonlit nights. These studies frequently overlooked a sequence of behaviors during the main peak of activities in the first hours of the night. We describe and quantify the nocturnal activities of a nesting Common Potoo based on continuous observations using an infrared digital camera.

METHODS

Study Area.—The study was conducted on the edge of the Universidade Estadual Paulista campus (22° 23′ 57.7″ S, 47° 32′ 13.5″ W), municipality of Rio Claro, southeastern Brazil. The nest site was in transitional vegetation among a small 0.5-km² fragment of disturbed scrub native savanna cerrado and a 25-km² fragment of secondary dry forest mixed with non native Pinus spp. and Eucalyptus spp. trees on the east side. The study site is considered an urban area as the closest populated area is <1 km to the west.

Data Collection.—Data were collected on 8, 12, 13, and 16 December 2008. We used an infrared digital Sony DSC H9 camera on a tripod hidden in a small bush ~ 1 m from the fence post where the Common Potoo nested. A wire frame and an additional infrared diode system were installed next to the camera to improve image quality during recordings.

Recording sessions were initiated at dusk and continued after 1900 hrs when the potoos started their nocturnal activities (Table 1). The maximum length of recordings was ~3 hrs. We used two batteries on some days with nearly 1.5 hrs of recording capacity on each. Immediately before the first battery quit, a person quietly approached the nest to change the batteries.

Digital recordings were analyzed in the laboratory and the following categories of behavior were recorded while the nestling was alone in the nest...
or accompanied by one of the parents: (1) feeding bouts on passing insects, (2) defecations, (3) movements in the nest, (4) wing exercising, (5) plumage maintenance, and (6) calling. Feeding bouts to capture insects were used by the nestling and adults while they were perched on the nest (on the top of the fence post) and attacked flies that were passing. Defecation behavior was perceived when the nestling raised the tail and ejected feces from the nest. Movements on the nest were used by the nestling to move short distances (several centimeters) from border to border of the stump. Wing exercising was used by the nestling apparently to exercise without flying. Plumage maintenance with the beak was used by the nestling and adults. Calls were used in a parental interaction and included begging notes uttered by the nestling and advertisement calls uttered by adults. We quantified the frequency per hour of each of these categories.

We verified the amount of time the nestling and each parent remained in alert posture, the frequency and times that each parent left the nest, and the number of times they alternated care and fed the nestling through regurgitation. The alert posture was adopted when nestling or adults raised their beak, compressed the plumage, and kept the neck outstretched (Fig. 1). Common Potoos do not show any sexual dimorphism (Cohn-Haft 1999). However, we noted a difference in the pattern of dark blotches on the breast of the two adults (hereafter indicated as individuals A and B) that enabled us to identify shared parental care.

RESULTS

Description of the Nest, Egg, Nestling, and Parents.—A Common Potoo responded to a playback of its call by vocalizing during a nocturnal bird survey and perched on a fence post on 4 November 2008. The potoo could be closely approached and another visit to the site was made 2 days later to confirm the existence of a nest. The simple and unlined nest contained a single dull white egg with lilac and brown spots (40.95 x 31.55 mm). It was directly placed on top of a 1.25-m tall abandoned fence post. The top of the post had an irregular surface that measured 5 x 19 cm (Fig. 1).

Presence of the nestling with an egg tooth and eggshell fragments in the nest indicated hatching occurred between 22 and 24 November. The nestling was covered by creamy-white down plumage marked with fine gray brown stripes on the first recording day (8 Dec). It was ~ one-third of the size of an adult at this time and could stay completely hidden among the ventral feathers of the parent (Fig. 1). The nestling was slightly more than half the size of an adult on the last day of recording (16 Dec), and remained almost completely exposed even when among the ventral feathers of the adult. Adults had a buff plumage with light gray and black blotches. The same gray-brown stripes of the nestling were also apparent along the adult’s body. A visit to the nesting site on 21 December revealed the nestling had probably been predated and the adults were no longer present.

Quantitative Aspect of Categories of Behavior.—Digital recordings (9 hrs and 6 min) were made when the nestling was ~14–16 days until 22–24 days of age (Table 1). Adults stayed with the nestling during nearly 5 hrs and 54 min (64.8% of total recording time) and the time the parents brooded the nestling decreased as it became older (Fig. 2).

The adult present gradually relaxed to a less motionless posture and slowly opened its eyes at nightfall. It completely opened its eyes at ~1854 to 1908 hrs and initiated nocturnal activities, flying from the nest between 1904 to 1909 hrs. Generally, the nestling became active from the motionless posture similarly to the adult.

The nestling engaged in feeding bouts on passing flies and flapped its wings only when alone after the first day of recording. Frequencies of short movements on the nest and plumage maintenance were also higher when the nestling
FIG. 1. Nest of Common Potoo (Nyctibius griseus) with adult (on the left) and nestling covered by creamy-white down plumage (on the right) in a typical alert posture. Lower right corner = frame taken with the infrared camera showing the nestling (on the left) being fed by adult B (on the right) on 12 December. Note the eye and beak of the adult.

FIG. 2. Brooding (% of time) of the nestling Common Potoo by an adult as a function of age.
was alone. The nestling vocalized much more frequently while accompanied by one of the parents than when alone (Table 2).

Adults A and B stayed in the nest for 1 hr and 59 min (17.5% of total recording time), and 4 hrs and 17 min (47.2% of total recording time), respectively. A change-over between adults at the nest was recorded four times: day 1 at 2028 hrs; day 2 at 2155 hrs; and day 3 at 1919, and 2115 hrs. Both adults left the nest six and 13 times during the sampled period: adult A (day 1 at 2030 hrs; day 2 at 1957 and 2056 hrs; day 3 at 1919 and 2115 hrs; and day 4 at 1927 hrs), and adult B (day 1 at 1931, 1935, 2008, and 2209 hrs; day 2 at 2055, 1940, and 2137 hrs; day 3 at 1909, 1919, 1942, and 2131 hrs; and day 4 at 1904 and 1923 hrs). Adults also fed on passing insects while perched in the nest, but only adult B called once. The frequency of food regurgitation to the nestling was similar between adults (Table 3). The nestling, adult A, and adult B adopted the alert posture during nearly 5 min and 24 sec (1.0% of total sampled time), 2 min and 24 sec (0.4%), and 1 hr and 48 min (19.8%) of video recording, respectively.

**DISCUSSION**

The infrared recording sessions enabled us to analyze and quantify behaviors of nestling and adult Common Potoos during the darkest nights. Parental attendance at the nest decreased as the nestling grew. Skutch (1970) and Tate (1994) reported that 25 days after hatching, adults were no longer staying with the nestling at the nest. They also reported that until nearly 50 days of age, the fledgling moved frequently with short flights, and the adults fed it in surrounding areas. Some behaviors of Common Potoo recorded in our study were also reported elsewhere, but rarely quantified, including: brief movements of the nestling in the nest (Tate 1994); wing exercising (Skutch 1970); alert posture (Muir and Butler 1925, Skutch 1970, Tate 1994); calling of the nestling and adults at the nest (Muir and Butler 1925, Skutch 1970, Corbo and Macarrão 2010); adults feeding the nestling by regurgitation (Skutch 1970, Corbo and Macarrão 2010); and alternation of adults at the nest (Lopes and Anjos 2005). Other behaviors of the potoos we observed are described for the first time, including: feeding bouts on passing insects by both the nestling and adults while sitting in the nest; defecation, and plumage maintenance by the nestling.

Brief movements on the nest by the nestling were performed when it was alone. Tate (1994) also observed nesting movements on a nest in Venezuela. We observed the nestling moved mainly to empty space left by the adult when it flew from the nest. One explanation for brief movements might be the improvement of blood circulation considering the great motionless period of the nestling during the day (Cohn-Haft 1999). The nestling flapped its wings at times for a few seconds after or before moving, probably as a way to exercise its pectoral muscles. This wing exercising started when the nestling was 14 days of age, 2 days earlier than mentioned by Skutch (1970) in Costa Rica.

The adults and nestling relied on the motionless alert posture during most of the day and in threatening situations during the night (Skutch 1970). We noted that a noise caused by a person near the nest site immediately modified the relaxed posture to an alert posture. We also observed the adult slowly turning its head to keep the intruder in focus in agreement with Muir and Butler (1925), Skutch (1970), and Tate.

**TABLE 2.** Frequency per hour (total recording time = 9 hrs and 6 min) of behavioral activities by Common Potoo nestling when alone at the nest and when accompanied by an adult.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Alone</th>
<th>Accompanied</th>
</tr>
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<tbody>
<tr>
<td>Feeding on passing flies</td>
<td>1.87</td>
<td>0</td>
</tr>
<tr>
<td>Defecation</td>
<td>0.31</td>
<td>0.34</td>
</tr>
<tr>
<td>Brief movements</td>
<td>6.25</td>
<td>2.38</td>
</tr>
<tr>
<td>Wing flapping</td>
<td>4.06</td>
<td>0</td>
</tr>
<tr>
<td>Plumage maintenance</td>
<td>4.37</td>
<td>1.70</td>
</tr>
<tr>
<td>Vocalization (calls)</td>
<td>4.37</td>
<td>647.1</td>
</tr>
</tbody>
</table>

**TABLE 3.** Frequency per hour (total recording time = 9 hrs and 6 min) of behavioral activities by adult Common Potoos (A and B) at the nest.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Adult A</th>
<th>Adult B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest leaving</td>
<td>3.77</td>
<td>1.86</td>
</tr>
<tr>
<td>Feeding on passing insects</td>
<td>8.18</td>
<td>0.70</td>
</tr>
<tr>
<td>Calling</td>
<td>0</td>
<td>0.93</td>
</tr>
<tr>
<td>Feeding of nestling</td>
<td>2.52</td>
<td>2.10</td>
</tr>
</tbody>
</table>
The nestling and adult gradually returned to the relaxed position, if left undisturbed for ~10 min. During relaxed situations, and when the nestling was on its own in the nest, it frequently engaged in feeding on passing flies and in maintaining its plumage. We did not perceive if the nestling captured prey during the faster feeding bouts, but this foraging behavior may be important in the early stages of species maturation as it optimizes food intake by the nestling in periods of absence of adults. Preening is also important to get rid of mites and lice (Cohn-Haft 1999). Adults performed the same behaviors when they were sitting in the nest. Feeding bouts of adults while perched are a way to supplement their diet without flying and abandoning its primary defense of inconspicuousness.

Defecation was another observed care behavior of the nestling. This occurred when the nestling raised its tail and ejected feces 30 to 50 cm from the nest. The absence of feces in and near Common Potoo nests has been reported (Skutch 1970, Sick 1993, Cohn-Haft 1999, and Lopes and Anjos 2005). This behavior should reduce the risk of predation and presence of parasites.

The nestling uttered a soft song while alone and on occasions that it was accompanied by one of the adults. This behavior has been reported in the literature prior to the arrival of an adult at the nest (Skutch 1970, Corbo and Macarrão 2010). Stronger calls in our study were also uttered by an adult when it approached the nest, probably to inform the nestling of its presence. The nestling increased the frequency of begging for food calls when an adult arrived at the nest, and when the adult fed it by regurgitation. Adults came to the nest three to 10 times to feed the nestling by regurgitation before midnight, similar to the observations of Skutch (1970) and Lopes and Anjos (2005). One of the parents (adult B) came more frequently to the nest, but we were not able to identify if it was male or female.

Cryptic plumage, inconspicuous behavior, and reduced activities around the nest are all adaptations to reduce attention to nesting potoos (Cohn-Haft 1999). The 51 days of the nestling period of the Common Potoo from hatching to young departure from the nest (Skutch 1970) is considered very long among birds (Sick 1993). The lower height of the nest in our study, in comparison with the interval from 3 to 15 m reported in other studies (Muir and Butler 1925, Haverschmidt 1958, Borrero 1970, Skutch 1970, Lopes and Anjos 2005, Greeney et al. 2008, Corbo and Macarrão 2010), possibly facilitated a predation event. However, several behaviors of the species led to the inconspicuousness during this time, and the long time of parental investment attest to their protective value for survival (Skutch 1970, Cohn-Haft 1999). New methods and technology to precisely study behaviors are needed. The use of infrared cameras in future studies would allow obtaining better insight of the nightly activities at the nest. Identification of the gender of adults would allow better study of how males and females share incubation and brooding duties.

ACKNOWLEDGMENTS

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LITERATURE CITED


ABSTRACT.—We collected observational data in three consecutive breeding seasons to study interactions between the botfly Philornis seguyi and Red-crested Cardinals (Paroaria coronata) in a temperate zone near the southern limit of Philornis distribution. We analyzed: (1) seasonal trends in prevalence of parasitism, (2) influence of botfly parasitism on nestling growth rate and survival, and (3) the association between nest site vegetation at different scales (i.e., nest tree, vegetation surrounding the nest tree, and landscape) and probability of botfly parasitism. Prevalence of parasitism was 28% and was higher later in the breeding season. Botfly parasitism produced sub-lethal (lower growth rate of nestlings that survive) and lethal (lower nestling survival) effects. The lethal effect was negatively associated with age at the time nestlings were parasitized. Botfly parasitism was not associated with vegetation characteristics at the level of nest tree or vegetation surrounding the nest tree, but was associated with landscape features. Parasite prevalence was higher in large continuous woodland patches than in small isolated patches. However, we did not observe increased use of isolated patches of forest by Red-crested Cardinals, suggesting that use of nest sites with high botfly parasite intensity could be the consequence of high host density. Received 6 April 2010. Accepted 19 October 2010.

Nestling birds are hosts to a wide range of ectoparasites that capitalize on the brief period of rapid host development and resource availability (Loye and Carroll 1995). Three dipteran families (Calliphoridae, Muscidae, and Piophilidae) represent most of the hematophagous parasites of birds (Uhazy and Arendt 1986, Ferrar 1987). Many species of the genus Philornis (botflies) within the Muscidae parasite nestlings and adults of cavity and open-nesting birds in the Neotropics (Arendt 1985a). Studies of the interactions between the genus Philornis and their hosts have been limited to a few species (i.e., P. downsi and Darwin’s finches in the Galápagos Islands) (Fessl et al. 2001; Fessl and Tebbich 2002; Fessl et al. 2006a; b; Dudaniec et al. 2006; Dudaniec et al. 2007; Huber 2008; Kleindorfer and Dudaniec 2009; O’Connor et al. 2010c), or to species distributed in tropical and subtropical regions (Dudaniec and Kleindorfer 2006).

The genus Philornis includes ~50 species of flies, all ectoparasites of birds (Couri and Carvalho 2003, Dudaniec and Kleindorfer 2006). The life cycle of most of these species as well as relationships with their hosts is frequently unknown (Couri 1999, Teixeira 1999, Dudaniec and Kleindorfer 2006). Flies of this genus are distributed from central Argentina to the southern United States (Couri 1999, Fessl et al. 2001). Botflies have been reported to parasitize at least 127 species of birds without marked host specificity (Couri 1991, Teixeira 1999). Most botfly species have subcutaneous larvae (Couri et al. 2005) and nestlings can be parasitized as soon as they hatch (Arendt 1985b; Delannoy and Cruz 1988, 1991; Spalding et al. 2002; Rabuffetti and Reboreda 2007). Botfly larvae feed on red blood cells (Uhazy and Arendt 1986) and remain in nestlings for 5-8 days (Arendt 1985b, Young 1993, Rabuffetti and Reboreda 2007, Quiroga 2009) when they leave the nestling as third instars and pupate in nest material (Uhazy and Arendt 1986). Adult flies emerge after a pupation period of 1–3 weeks (Oniki 1983, Young 1993, Rabuffetti and Reboreda 2007, Quiroga 2009).

Most studies indicate botfly parasitism produces sublethal (i.e., lower growth rates) or lethal effects on their hosts (Arendt 1985a, b; Delannoy and Cruz 1991; Young 1993; Fessl and Tebbich 2002; Rabuffetti and Reboreda 2007). One of the predictor variables for nestling survival is parasite intensity (number of larvae/nestling) (Dudaniec and Kleindorfer 2006). Some studies have reported only 5–6 larvae caused nestling death (Arendt 1985b, Delannoy and Cruz 1991), but others report similar intensities were not lethal (Nores 1995) and were only associated with lower growth rates (Young 1993). The other variable that influences nestling survival is age at the time they are parasitized (Arendt 1985a, 2000; Rabuffetti and Reboreda 2007) although this association has been less studied. Parasite prevalence (the percentage of nests with larvae) increases as the
host breeding season advances (Arendt 1985a, b; Young 1993; Rabuffetti and Reboreda 2007), although some studies did not find a trend (Nores 1995, Fessl and Tebbich 2002, Quiroga 2009).

The role of nest-site vegetation on prevalence and intensity of botfly parasitism has received little research attention, except for the work of O'Connor et al. (2010a) who reported higher prevalence and intensity of botfly (P. downsi) parasitism in moist forest highlands than in arid lowlands of the Galapagos Islands and suggested that size and continuity of forest patches could influence botfly dispersal ability. Understanding the role of nest-site vegetation on parasite infestation may help predict the likelihood of parasitism for a given host in a given environment (Loye and Carroll 1998).

We used a large set of observational data collected during three consecutive breeding seasons to study the interactions between Philornis seguyi and Red-crested Cardinals (Paroaria coronata), a species that has been previously reported as a host of botflies in central Argentina (De la Peña et al. 2003). We examined: (1) seasonal trends in parasite prevalence and intensity, (2) the influence of botfly parasitism on nestling growth and survival, and (3) the association between nest-site vegetation at different scales and probability of botfly parasitism. We hypothesized that survival of Red-crested Cardinal nestlings may be negatively associated with parasite intensity and positively associated with age at time of parasitism. We expected nests in small isolated patches of forest would have lower parasite prevalence than those in large continuous patches, because grassland areas that separate isolated from continuous patches may act as barriers for dispersal.

METHODS

Study Site.—The study was conducted near the town of Punta Indio, Buenos Aires Province, Argentina (35°20' S, 57°11' W). The vegetation at the study site consists of woodlands arranged in several strips (50–100 m in width and up to several km in length) parallel to the edge of the “de la Plata” River surrounded by small areas of grassland. In addition, there are also small patches of forests (between 10 and 70 m in diameter) more distant from the edge of the river surrounded by large areas of grassland. These small patches are separated from woodland strips by 300–1,200 m. The woodlands are dominated by Celtis tala (Tala) and Scutia buxifolia (Coronillo). The annual rainfall for the study site is 891 mm and rainfall during the study period varied between 772 (2005) and 845 mm (2007). We collected data during Red-crested Cardinal breeding seasons (early Oct-mid Feb) 2005–2006 to 2007–2008. Average annual rainfall during the breeding season is typically 441 mm and, during the breeding seasons of 2005–2006, 2006–2007, and 2007–2008, it was 431, 439, and 487 mm, respectively. Ranges of mean monthly ambient temperatures during the study period were 14.8 (Oct) to 21.9°C (Jan) in 2005–2006, 17.0 (Oct) to 23.2°C (Feb) in 2005–2006, and 17.1 (Oct) to 24.6°C (Jan) in 2007–2008.

Study Species.—Red-crested Cardinals inhabit semi-open areas with scattered trees and shrubs from east central Argentina to southern Brazil, Paraguay, eastern Bolivia, and Uruguay (Ridgely and Tudor 1994). Their nests at our study site were at a height of 2–6 m, primarily in Tala and secondarily in Coronillos and Molles (Schinus longifolius) (Segura and Arturi 2009). Nests are open-cups with external and internal diameters of 13 and 6.5 cm, respectively, a depth of 4.5 cm and lateral translucent walls of 2 cm in width (LNS, unpubl. data). The wall of the nest is built with thin dry branches of Tala and small stems of grass while the chamber is lined with thin rootlets, vegetation fibers, and cattle hair. Clutch size varies between two and four eggs, nestlings hatch after 12 days of incubation and fledge ~14 days after hatching (LNS, unpubl. data). Average mass of nestlings at hatching is 3–3.5 g and 30–31 g at time of fledging (LNS, unpubl. data).

The species of botfly recorded previously in our study area is P. seguyi (Couri et al. 2005, Rabuffetti and Reboreda 2007). We collected botfly larvae from Chalk-browed Mockingbird (Mimus saturninus, n = 21), House Wren (Troglodytes aedon, n = 9) and Baywing (Agelaioides badius, n = 3) nestlings, all identified (Martin Quiroga, INALI-CONICET, Argentina) as P. seguyi (Garcia 1952, Couri et al. 2009). Quiroga (2009) described the life cycle of this species. P. seguyi larvae feed and develop subcutaneously in the host for 5–6 days reaching a length of ~8–9 mm and a mass of 0.11–0.13 g. Larvae drop from the host to undergo pupation, emerging as adult flies after 9–10 days. Host larvae do not pupate at the bottom of the nest due to the scarce material that forms the cardinal nest, but drop to the ground where they undergo pupation (LNS, unpubl. data).
Data Collection.—Nests were found by searching systematically in potential nest sites and by observing nesting behavior of territorial pairs (Martin and Geupel 1993) of Red-crested Cardinals. We found 367 nests ($n = 108, 120,$ and 139 for the breeding seasons of 2005–2006, 2006–2007, and 2007–2008, respectively). Nearly 50% of the nests ($n = 177$) were found during construction and laying with the remainder found during incubation ($n = 152$) and after hatching ($n = 38$). We used 131 nests that survived at least 6 days after the first nestling hatched ($n = 36, 45,$ and 50 for 2005–2006, 2006–2007, and 2007–2008, respectively). We used this criterion in our study because botfly parasitism occurred while nestlings were between 1 and 6 days of age. Inclusion of nests depredated before nestlings were 6 days of age would result in underestimation of parasite prevalence.

Nests were checked daily until all eggs hatched and then every 2 days until the nestlings fledged or the nest failed. Nestlings were marked after hatching on the tarsus with black ink for or the nest failed. Nestlings were marked after and then every 2 days until the nestlings fledged construction and laying with the remainder found during incubation ($n = 152$) and after hatching ($n = 38$). We used 131 nests that survived at least 6 days after the first nestling hatched ($n = 36, 45,$ and 50 for 2005–2006, 2006–2007, and 2007–2008, respectively). We used this criterion in our study because botfly parasitism occurred while nestlings were between 1 and 6 days of age. Inclusion of nests depredated before nestlings were 6 days of age would result in underestimation of parasite prevalence.

We measured body mass with 30 and 50 g Pesola spring scales (accuracy ± 0.2 and ± 0.5 g, respectively). Length of the tarsus and beak with a dial caliper (accuracy ± 0.001 mm), and length of the wing with a ruler (accuracy ± 0.001 mm). We minimized the effect of daily variation in body mass and size by collecting these data between 1600 and 1900 hrs.

We analyzed the structure of the vegetation surrounding the nest by measuring vegetation characteristics at three different scales: (1) nest tree, (2) vegetation surrounding the nest tree, and (3) landscape. We measured (1) tree species, (2) nest height, (3) distance from the nest to the edge of the canopy, and (4) cover of the canopy at the nest tree scale. We measured the cover of tree canopy within a 15-m radius of the nest at the surrounding nest tree vegetation scale, and whether the nest tree was in the continuous strips of forest parallel to the river or in small isolated

Data Analysis.—We assumed a nest was successful if it fledged at least one young and depredated if all nestlings disappeared between two consecutive visits. We did not observe abandonment of nests with nestlings in circumstances other than botfly parasitism. We assumed that a nestling died as a result of botfly parasitism if it was previously parasitized and found dead or disappeared between visits with no evidence of attack by predators (i.e., feathers or blood in the nest).

We estimated the lethal effect of botfly parasitism by comparing nestling survival (proportion of nestlings that fledged) between non- and parasitized nests excluding nests that were depredated. We estimated the sub-lethal effects of botfly parasitism by comparing growth rates of: (1) body mass, (2) tarsus length, (3) beak length, and (4) wing length between non- and parasitized chicks that survived. We used brood means to avoid pseudoreplication. We calculated growth rates as the slope of a linear regression of the values of each variable versus age of nestlings between 2 and 8 days of age (hatching day = age 0). Growth rates of all the variables were almost linear for nestlings 2–8 days of age (body mass: $y = 3.0 x + 1.6$, $r = 0.99, P < 0.001$; tarsus length: $y = 2.1 x + 5.9$, $r = 0.99, P < 0.001$; beak length: $y = 0.56 x + 4.9$, $r = 0.99, P < 0.001$; and wing length: $y = 4.7 x - 0.79$, $r = 0.99, P < 0.001$; $n = 222$ data points from 66 non-parasitized nests). We only considered nests in which we had three or more measurements in that period (16 parasitized and 66 unparasitized nests). We used nests with nestlings during January and February only for analysis of the association between vegetation characteristics and botfly parasitism, as the occurrence of parasitism in nests with nestlings during the previous months was practically zero.

We used parametric tests for normally distributed data only, and nonparametric tests with corrections for ties. We used Mann-Whitney $U$ or Kruskal-Wallis tests for independent comparisons. We used logistic regressions to analyze the association between botfly parasitism (binary dependent variable) and one or more independent
TABLE 1. Parasite prevalence (percentage of nests parasitized), parasite intensity (mean number of larvae/nestling and per nest), latency of parasitism (time elapsed since hatching of the first nestling and nest parasitism), and date first brood of Red-crested Cardinals was parasitized for three breeding seasons (2005–2008) in central Argentina woodlands.

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<tr>
<td>Parasite prevalence</td>
<td>8/36 (22.2%)</td>
<td>12/45 (26.7%)</td>
<td>17/50 (34%)</td>
</tr>
<tr>
<td>Parasite intensity</td>
<td>14.4 ± 1.6</td>
<td>10.8 ± 1.8</td>
<td>13.4 ± 1.7</td>
</tr>
<tr>
<td>(± SE of larvae/nest)</td>
<td>(range: 9–22)</td>
<td>(range: 3–26)</td>
<td>(range: 3–29)</td>
</tr>
<tr>
<td>Parasite intensity (± SE of larvae/nestling)</td>
<td>6.7 ± 1.3</td>
<td>6.5 ± 1.4</td>
<td>6.4 ± 0.9</td>
</tr>
<tr>
<td>(± SE of age of nestlings)</td>
<td>(range: 4.5–16)</td>
<td>(range: 2.5–19)</td>
<td>(range: 1.7–16)</td>
</tr>
<tr>
<td>Latency of parasitism</td>
<td>3.0 ± 0.38</td>
<td>3.3 ± 0.35</td>
<td>3.2 ± 0.39</td>
</tr>
<tr>
<td>(± SE of age of nestlings)</td>
<td>(range: 2–5)</td>
<td>(range: 2–6)</td>
<td>(range: 1–6)</td>
</tr>
<tr>
<td>Date first brood parasitized</td>
<td>10 Jan</td>
<td>31 Dec</td>
<td>11 Jan</td>
</tr>
</tbody>
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variables. We used Fisher's exact or Chi-square tests for the analysis of contingency tables. Reported values are means ± SE. All tests were two-tailed and differences were considered significant at $P < 0.05$. Statistical tests were completed using STATISTICA 7.0 (StatSoft Inc. 2004).

RESULTS

Prevalence and Intensity of Parasitism during the Breeding Season.—The prevalence of botfly parasitism was 28.2% (37/131 nests) and did not differ between years ($X^2 = 0.85$, $P = 0.65$; Table 1). There was a positive association between occurrence of botfly parasitism and time of breeding for the three breeding seasons (logistic regressions: 2005–2006, $X^2 = 14.2$, $P < 0.001$; 2006–2007, $X^2 = 17.1$, $P < 0.001$ and 2007–2008, $X^2 = 36.1$, $P < 0.001$) with most parasitized nests (36/37) occurring in January and February (Fig. 1). We divided the breeding season into 15-day intervals and calculated the proportion of nests that were parasitized with botflies for each interval to examine if the seasonal increase in parasite prevalence during January and February was associated with a decrease in availability of nests. We combined the data for the 3 years because of the small number of periods per year. There was no significant association between number of nests with nestlings and botfly prevalence (Spearman’s rank correlation: $r = -0.20$, $P = 0.52$, $n = 12$; Fig. 1). All nestlings were parasitized in 35 of 37 nests. Botfly intensity was $6.5 \pm 0.66$ larvae/nestling (range: 1.6–19, $n = 37$ nests; Fig. 2A) and was not statistically different between years (Kruskal-Wallis test: $H_2 = 3.4$, $P = 0.18$, $n = 37$) and was not associated with date of hatching (Spearman’s rank correlation: $r = 0.1$, $P = 0.55$, $n = 37$). Latency of parasitism (time elapsed since hatching of the first nestling and nest parasitism) was $4.2 \pm 0.2$ days (range 2–6 days, $n = 35$ nests; Fig. 2B) and did not differ across years (Kruskal-Wallis test: $H_2 = 0.6$, $P = 0.74$; Table 1).

Lethal and Sub-lethal Effects of Botfly Parasitism.—Thirteen of 37 nests parasitized by botflies were depredated and excluded from analysis of nestling survival. No nestlings fledged in 4/24 nests (17%), there was partial fledging (some nestlings fledged, some died) in 7/24 nests (29%), and all nestlings fledged in 13/24 nests (54%). Nestling survival was lower in parasitized than in non-parasitized nests (parasitized: $0.6 \pm 0.07$, $n = 35$; non-parasitized: $0.8 \pm 0.05$, $n = 32$).

FIG. 1. Botfly parasitism of Red-crested Cardinals at different times of the breeding season in Buenos Aires Province, Argentina. White circles show the number of nests that produced nestlings during the 15-day interval and black circles = the percentage of those nests parasitized by botflies. Data correspond to the breeding seasons of 2005–2006, 2006–2007, and 2007–2008 combined ($n = 131$ nests).
Characteristics of the Vegetation and Botfly Parasitism.—We did not detect a significant association between occurrence of botfly parasitism and species of nest trees (Tala: 22/44; Coronillo: 15/23; $\chi^2 = 0.04$, $P = 0.52$). We also did not observe a significant association between botfly parasitism and other characteristics of the vegetation at the nest-tree level (logistic regressions for nest height: $\chi^2 = 1.24$, $P = 0.26$; distance from the nest to the edge of the canopy: $\chi^2 = 0.04$, $P = 0.83$; and cover of the canopy:

Predation outcome did not differ between parasitized and non-parasitized nests ($X^2_1 = 0.33$, df = 1, $P = 0.56$) for the three breeding seasons combined. Young that fledged from parasitized nests had lower growth rates for body mass (Fig. 4A), tarsus length (Fig. 4B), beak length (Fig. 4C), and wing length (Fig. 4D) than young that fledged from non-parasitized nests (Mann-Whitney U-test; body mass: $Z = -2.94$, $P = 0.003$; tarsus length: $Z = -3.02$, $P = 0.002$; beak length: $Z = -2.54$, $P = 0.01$; wing length: $Z = -2.13$, $P = 0.03$).

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Botfly parasitism of Red-crested Cardinals increased during the breeding season, but was not significantly different across years. Parasite prevalence and intensity had lethal (lower nestling survival) and sub-lethal (lower growth rate of nestlings that survive) effects. Nestling survival in parasitized nests was positively associated with age at which nestlings were parasitized. In addition, botfly parasitism was more prevalent in nests in large continuous patches of riverine woodland than in small isolated patches further from the river.

Red-crested Cardinals start breeding in early October, but first records of botfly parasitism occurred in late December-early January. Similarly, Rabuffetti and Reboreda (2007), in a study conducted only 35 km north of our study site, observed low prevalence of botfly parasitism at the beginning of the Chalk-browed Mockingbird breeding season (mid Oct–early Dec), but high prevalence towards the end of the season (late Dec–Jan). Quiroga (2009) studied House Wrens 500 km north our study area and reported botfly parasitism in late October–November and did not detect any seasonal trend in parasite prevalence. It is likely our study site is close to the southern limit of the parasite's distribution, as studies of House Wrens (a regular host of botflies; Young 1993, Quiroga 2009) 100 km south of our study site did not detect parasitism (Llambias and Fernandez 2009; Paulo Llambias, pers. comm.).

This effect was less than reported by Arendt (1985b, Delannoy and Cruz 1991, Fessl and Tebbich 2002, O'Connor et al. 2010c), who found the distribution of flies of the genus Protopaliphora increased over the breeding season because new adults emerge while older flies persist. Thus, as the season advances, the number of adult flies increases which would explain the finding of higher parasite prevalence.

Many studies report parasitic botflies (Philornis spp.) have detrimental effects on nestling survival (Arendt 1985b, Delannoy and Cruz 1991, Fessl and Tebbich 2002, O'Connor et al. 2010c), growth (Young 1993), and malformation that may persist in adults (Galligan and Kleindorfer 2009). Our results conducted in a temperate area close to the southern limit of the parasite's distribution could be the result of lower ambient temperatures that delay emergence of new adults early in the season. Bennett and Whitworth (1991a, b) reported population size of flies of the genus Protopaliphora increased over the breeding season because new adults emerge while older flies persist. As such, as the season advances, the number of adult flies increases which would explain the finding of higher parasite prevalence.

FIG. 4. Growth rates of (A) body mass (g × day\(^{-1}\)), (B) tarsus length (mm × day\(^{-1}\)), (C) beak length (mm × day\(^{-1}\)), and (D) wing length (mm × day\(^{-1}\)) for Red-crested Cardinal nestlings that fledged from unparasitized nests (NP, \(n = 66\)) and from nests parasitized by \(P. \) seguyi botflies (P, \(n = 16\)). Growth rates were estimated as the slope of the linear regression between the values of each variable and the age of nestlings between 2 to 8 days of age (hatching day = age 0).

\[ X^2_1 = 0.86, P = 0.35; n = 67, \]

or at the level of vegetation surrounding the nest tree (logistic regression: \( X^2_1 = 2.67, P = 0.1, n = 67\)). There was a significant effect of landscape features and botfly parasite prevalence; nests in connected riverine woodlands had higher parasite prevalence than nests in small woodland patches more distant from the river (large riverine woodlands patch: 32/46 nests; small woodlands patch: 5/21 nests; \( X^2_1 = 4.0, P = 0.04\)).

**DISCUSSION**

Botfly parasitism of Red-crested Cardinals is likely our study site is close to the southern limit of the parasite's distribution approach the southern limit of the parasite's distribution could be the result of lower ambient temperatures that delay emergence of new adults early in the season. Bennett and Whitworth (1991a, b) reported population size of flies of the genus Protopaliphora increased over the breeding season because new adults emerge while older flies persist. Thus, as the season advances, the number of adult flies increases which would explain the finding of higher parasite prevalence.

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impact of botfly parasitism on host nesting survival between studies may be due to differences in parasite intensity, which was three-fold higher in meckingbirds than in cardinals.

Latency of parasitism, as in other studies (Arendt 1985a, 2000; Rabuffetti and Reboreda 2007), was an important factor that influenced nestling survival. We found a positive relationship between nestling survival and age at time of parasitism. We also observed a negative association between latency and parasite intensity. The latter association possibly indicates that changes in the skin of nestlings as they grow (likely the presence of feathers after day 5–6) may prevent larvae from penetrating the skin. We did not find an association between nestling survival and parasite intensity, probably due to low intensity in this study.

Nests in large continuous forest along river edges were more parasitized than those in small isolated patches, even when the distance between both types of patches was a few hundred meters. Bennett and Whitworth (1991b), in an experimental study with adult flies of the genus Protocaliphora, found that adult flies do not move large distances and that new infestations occur <50 m from where adults emerged. Dudaniec et al. (2010) also found lower levels of genetic relatedness in *P. downsi* when nests where located in more arid environments and host nesting density was lower. Open areas of grasslands that separate patches of forest may act as barriers for botfly dispersal. Alternatively, isolated patches of forest could have microclimate conditions (i.e., lower humidity and higher temperatures) that may reduce their suitability for botflies. O'Connor et al. (2010a) found habitat differences in *Philornis* parasite prevalence and intensity with higher levels of parasitism in moist forest highlands than arid lowlands on Floreana Island, in the Galapagos.

Some authors have proposed birds should avoid selecting nesting sites where they are more exposed to parasites, and that selection for good sites would be the first line of defense against parasitism (Loye and Carroll 1991, 1998; O'Connor et al. 2010b). We did not observe behavior by Red-crested Cardinals that suggested increased use of isolated patches of forest and earlier onset of breeding to avoid the higher parasite prevalence typical of riverine forest patches. Use of nest sites with high botfly parasite intensity could be the consequence of high host density; we have observations of high nesting density of Red-crested Cardinals in riverine forest study sites (LNS, unpubl. data). Kleindorfer and Dudaniec (2009) and Kleindorfer et al. (2009) found an effect of high host nesting density on high *P. downsi* parasite intensity in the Galapagos Islands. Little is known about the role of parasite infestation for host nest site selection behavior; more studies on these interactions are needed.

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MUSCLE MEMBRANE PHOSPHOLIPID CLASS COMPOSITION IN WHITE-THROATED SPARROWS IN RELATION TO MIGRATION

JEREMY SPRINGER,1 EDWIN R. PRICE,1,2 RAYMOND THOMAS,1 AND CHRISTOPHER G. GUGLIELMO1

ABSTRACT.—We document seasonal changes in the ratio of phosphatidylcholine (PC) to phosphatidylethanolamine (PE) in pectoralis muscles of captive and wild White-throated Sparrows (Zonotrichia albicollis). We manipulated day length in captive sparrows to induce ‘winter’ or ‘migratory’ condition. The PC/PE ratio in these sparrows was 1.87 ± 0.11 (mean ± SE), and did not vary significantly between treatments. However, the PC/PE ratio was higher in wild adult sparrows in winter (1.90 ± 0.19) than those caught in migration (1.20 ± 0.13 in spring; 1.37 ± 0.14 in fall). No effect of migratory state on PC/PE ratio was found among wild juveniles (1.32 ± 0.09 in fall, 1.18 ± 0.14 in winter). Seasonal changes to PC/PE ratios may be a result of migratory exercise, rather than migratory condition per se. Received 30 April 2010. Accepted 23 September 2010.

Findings of several recent studies have generated increased interest in muscle membrane alterations during exercise and how changes in membranes affect exercise performance (Ayre and Hulbert 1997, Infante et al. 2001, Guglielmo et al. 2002, Valencak et al. 2003, Nagahuedi et al. 2009). Ornithologists, in particular, have been interested in how membrane composition could affect migration, a period of high-intensity endurance exercise (Guglielmo et al. 2002, Price et al. 2010). Biological membranes are composed primarily of phospholipids which consist of a polar head group, a glycerol phosphate backbone, and two fatty acid tails. Exercise is known to affect both the fatty acid and head group moieties (class composition) of phospholipids in mammals and birds (Morgan et al. 1969, Ayre et al. 1998, Goski et al. 1999, Mitchell et al. 2004, Turner et al. 2004, Price et al. 2010). Changes to membrane fatty acid composition brought about by dietary manipulation have been associated with exercise performance alterations in mammals, fish, and birds (Ayre and Hulbert 1997, McKenzie et al. 1998, Pierce et al. 2005), although the role of membranes in these studies has been questioned (Price and Guglielmo 2009). Variation in the fatty acid composition of muscle membranes has been investigated in relation to migration (Guglielmo et al. 2002, Maillet and Weber 2006, Klaiman et al. 2009), but phospholipid class composition has not been studied in a migratory context. Our objective is to provide a first description of phospholipid class composition in migratory birds and how it changes seasonally, using photoperiod-manipulated captive birds as well as wild-caught migrating and wintering birds.

METHODS

Photoperiod-manipulated Captive Sparrows.—White-throated Sparrows (Zonotrichia albicollis) are short-hop, long-distance migrants common to eastern North America. Twelve White-throated Sparrows were captured near Long Point, Ontario by mist-netting in October. All birds were housed singly in 40 (height) × 45 × 45-cm cages, and were initially exposed to short day (8L:16D) photoperiod for 8 weeks to break photorefractoriness (Agatsuma and Ramenofsky 2006). Small night lights were used during the dark periods to avoid complete darkness. Birds were initially fed...
standard bird seed and then weaned onto a ground commercial diet (Mazuri small bird maintenance, PMI Nutrition International, Brentwood, MO, USA) over 4 weeks. Food and water were changed on a daily basis and provided ad libitum. Room temperature ranged between 21 and 24°C.

Five sparrows, after short day exposure, were switched to long days (16L:8D) for 28 days to stimulate migratory behavior (Agatsuma and Ramenofsky 2006), while the remaining birds were kept on short days. Hyperphagia and nightly hopping (Zugunruhe; characteristic of captive birds in migratory condition) were demonstrated by long day animals (D. J. Cerasale, D. M. Zajac, and C. G. Guggielmo, unpubl. data). Short day and long day birds were euthanized by decapitation following anesthesia with isoflurane at the end of this period. Right pectoralis muscle samples were rapidly removed and flash frozen in liquid nitrogen prior to storage (−80°C). Nearly all birds could be classified as juvenile or adult by the extent of skull ossification (DeHaven et al. 1974). Protocols were approved by the University of Western Ontario Council on Animal Care Animal Use Subcommittee (protocol #2005-060-08) and appropriate collection permits were obtained from the Canadian Wildlife Service (CA 0170, CA 0230) and the U.S. Fish and Wildlife Service (MB758364-1 issued to F. R. Moore).

Wild Sparrows.—Migratory White-throated Sparrows were captured using mist nets in April (spring, n = 8) and October (fall, n = 26) near Long Point, Ontario. Eleven wintering sparrows were captured during January near Stoneville, Mississippi at the Delta Experimental Forest. Birds were anesthetized with isoflurane and euthanized by cervical dislocation. The right pectoralis muscle was removed and immediately frozen in liquid nitrogen. Samples were stored at −80°C until analysis. Age was classified as juvenile or adult (DeHaven et al. 1974).

Lipid Extraction and Analysis.—Lipids were extracted following a modified Folch procedure (Folch et al. 1957). Pectoralis samples (100 mg) were homogenized in 2.5 mL chloroform/methanol (2:1 v/v) containing 25 mg/L butylated hydroxytoluene. Lipid extracts were stored at −20°C. Total lipid extracts were centrifuged (2,056 g) for 15 min, 1 mL of a mix of polar standards containing PC (L-α-phosphatidylcholine, Type XVI-E ~99%, Sigma), PE (L-α-phosphatidylethanolamine, Type III: from egg yolk ~98%, Sigma), sphingomyelin, and PS. Standard curves were developed using phospholipid standards (PC and PE). Area count data for PC and PE were normalized based on the recovered internal standard, and were used for the final calculation of PC/PE ratios.

Statistical Analysis.—The statistical significance level was set at α = 0.05 for all statistical tests. SPSS software (Version 17, SPSS Inc., Chicago, IL, USA) was used for all analyses. Student’s t-tests were used to examine the effect of season on the PC/PE ratio in captive sparrows. A general linear model was used to test for effects of season and age, and their interaction on PC/PE ratios in wild birds. Student-Newman-Keuls test was used to examine differences among groups in wild birds.
FIG. 1. Effects of migratory condition on muscle membrane PC/PE ratio in captive White-throated Sparrows subjected to photoperiod manipulation. There is no significant difference in the PC/PE ratios between long day (migratory) and short day (non-migratory) sparrows. Sample sizes for each group are presented across the top. Data are means ± SE. A single long day adult had a PC/PE ratio of 3.42.

FIG. 2. Effects of season and age on the muscle membrane PC/PE ratio in free-living White-throated Sparrows. There was a significant interaction between season and age. *Wintering adults had a higher PC/PE ratio than adults in other seasons (P < 0.05). Sample sizes for each group are presented across the top. No juveniles were caught in spring. Data are means ± SE; samples with unknown age are not shown. Two more wintering sparrows of unidentified age had PC/PE ratios of 2.1 and 3.4, and two more fall sparrows of unidentified age had PC/PE ratios of 1.41 and 1.17.

RESULTS

TLC-FID clearly resolved the phospholipid classes in the standard mix. The only measurable phospholipids in the muscle samples were PC and PE; we therefore concentrated our analyses on the ratio of PC to PE. The total PC concentration exceeded the total PE concentration in 89% of wild sparrows and 100% of captive sparrows.

Age was not investigated as a factor influencing the PC/PE ratio in captive birds because only one of the captives was an adult; this bird had a notably high PC/PE ratio (3.42). The PC/PE ratio among captive sparrows did not vary by photoperiod treatment (P = 0.34; Fig. 1). The PC/PE ratio varied significantly with season and age among free-living sparrows, but there was a significant interaction between age and season (P = 0.032). There was no significant effect of season within juveniles (P = 0.48) but, within adults, wintering birds had higher PC/PE ratios than migrants (P < 0.05, Fig. 2). Body mass had no effect when included as a covariate in the analysis.

DISCUSSION

Common polar head groups include serine, inositol, choline, and ethanolamine, but only the latter two are found in high concentrations in skeletal muscle (Mitchell et al. 2007); our results are in accordance with this previous observation. PC has a relatively large head group in relation to its fatty acid moieties, and forms a cylindrical molecular shape. Conversely, PE has a relatively small head group in relation to its fatty acid moieties, which results in a conical molecular shape and destabilizes membranes, making them more fluid (Logue et al. 2000). We focused on the ratio of PC/PE because the balance of these two phospholipids is important in affecting membrane characteristics (Logue et al. 2000).

Membrane class composition may change adaptively for many reasons, including regulation of membrane fluidity, integrity, and interactions with membrane-bound proteins (Hazel 1995, Nagahuedi et al. 2009). Our results from wild sparrows are consistent with an increase in muscle membrane fluidity during migratory periods, although this may have been offset by a decrease in the double bond index of the fatty acid composition (Klaiman et al. 2009). It is unclear, however, why the season effect was only observed in adults.

Our results are not consistent with any endogenous change to phospholipid class compo-
sion associated with migratory condition. However, the lack of adults in the captive study may have precluded observation of the seasonal pattern demonstrated by wild birds. It is also possible the photoperiod manipulation caused the birds to display classic migratory behavior (Zugunruhe and hyperphagia), yet was not sufficient alone to induce changes in the PC/PE ratio. Seasonal changes to the PC/PE ratio may only be induced by the higher intensity training of migratory flight itself, rather than pre-migratory conditioning, as suggested previously for membrane fatty acid composition (Price et al. 2010). A training effect is plausible, given that Górska et al. (1999) found that PE increased relative to PC in the red gastrocnemius muscles of rats after exercise training.

Klaiman et al. (2009) concluded that diet was a greater factor than exercise or migratory condition in producing the patterns they observed in their study of seasonal changes in membrane fatty acid composition in White-throated Sparrows. Diet can affect phospholipid class composition as well (Innis and Clandinin 1981), and could explain the current results from wild birds, but only if adults and juveniles forage in different ways during winter. This is also supported by the high PC/PE ratios observed in the captive sparrows (relative to wild sparrows), as they were fed the same commercial diet that may differ from natural forage. Our study indicates that composition of phospholipid classes in muscle membranes can vary seasonally, but data linking phospholipid class compositional changes directly to migratory exercise or migratory condition, rather than diet variation, remain equivocal.

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GELOCATION TRACKING OF THE ANNUAL MIGRATION OF ADULT AUSTRALASIAN GANNETS (MORUS SERRATOR) BREEDING IN NEW ZEALAND

STEFANIE M. H. ISMAR,1,5 RICHARD A. PHILLIPS,2 Matt J. Rayner,1,3 and Mark E. Hauber1,4

ABSTRACT.—The long breeding period and high reproductive investment of seabirds make use of resource-rich foraging areas pivotal both during and between breeding seasons. We tracked adult Australasian Gannets (Morus serrator) from their New Zealand breeding colony at Cape Kidnappers to Australia during the non-breeding period to assess wintering behavior and migratory routes for this species. Data from three recovered geolocation sensor (GLS) tags showed that both a male and a female M. serrator, and a hybrid M. capensis × M. serrator migrated across the Tasman Sea to winter in Australian and Tasmanian coastal waters. Tracked birds covered distances of up to 13,000 km on their migration. These movements were consistent with historical records of band recoveries. Received 28 April 2010. Accepted 29 September 2010.

Adults of many seabird species, in systems with obligate biparental care, invest heavily during breeding (Brooke 2004). Life history theory predicts that parents must balance the costs of current reproduction with future attempts, and the availability of good foraging conditions is critically important (Quillfeldt et al. 2005, Rayner et al. 2008). This is especially true as the inter-breeding period may be a time of peak mortality in the breeding cycle (Barbraud and Weimerskirch 2003). Increasing attention has focused on assessing migration strategies and foraging areas of seabirds during the non-breeding period (Phillips et al. 2006, Bost et al. 2009, Catry et al. 2009), since emergence of economical archival low-impact geolocator sensor (GLS) loggers (Rayner 2007) with long battery lives (Afanasyev 2004, Shaffer et al. 2006).

The Australasian Gannet (Morus serrator) is a predominantly monogamous seabird with an obligately biparental system, endemic to Australia and New Zealand (Nelson 1978, Ismar et al. 2010a). Migration strategies, particularly of the New Zealand population, are poorly known. Large numbers of recoveries in Australia from banded New Zealand breeding gannets include only one record of a bird known to be of sufficient age to breed (5 years; Hitchcock and Carrick 1958). This suggests a westward migration during the non-breeding season from New Zealand. Single band recoveries from dead adult Australasian Gannets have been reported between 2007 and 2010 from several New Zealand locations: Opotiki, Bay of Plenty; Wellington, Shelley Bay; Fiordland, South Coast; as well as two band recoveries from the Cape Kidnappers breeding site, and two observations of marked live birds from a gannetry at Farewell Spit (Mala Nesaratnam, Department of Conservation, Wellington, NZ, pers. comm.). One recovery has been reported from Wollongong in New South Wales, Australia; the gannet had last been recorded in New Zealand as a fledgling.

Migration to warmer, more productive waters has been recorded for gannet fledglings from New Zealand (Ismar et al. 2010b) and for adults of the congeneric Northern Gannet (M. bassanus) and Cape Gannet (M. capensis) that breed at temperate latitudes (Nelson 1978, Kubetzki et al. 2009). Thus, we hypothesized that breeding adult Australasian Gannets from New Zealand migrate to similar wintering areas as conspecific fledglings. Our objectives were to: (1) test the hypothesis that adult New Zealand breeding Australasian Gannets migrate to Australia between breeding seasons and to provide the first detailed information on migration routes and timing, and (2) test the use of GLS devices to monitor wintering behavior of the species.

METHODS

Five breeding adult Australasian Gannets (which raised chicks in the 2007–2008 breed-
ing season, Ismar et al. 2010a) at the Plateau Colony, Cape Kidnappers Gannetry, New Zealand (39° 38' S, 177° 05' E) were equipped with GLS loggers (Phillips et al. 2004) on 21 February 2008 and 12 March 2008. Deployments were timed for close to fledging at this location (Ismar et al. 2010a). Devices were placed (l = left, r = right leg) on two male (M-77108 [I], A08 [r] and M-74777 [I], 777 [r]) and two female (M-77177 [I], A77 [r] and M-74768 [I], 768 [r]) Australasian Gannets. The fifth bird (M-77260 [r], B60 [I]) was the putative male offspring of a male Cape Gannet (M. capensis) and a female Australasian Gannet hatched in 2001-2002 (Robertson and Stephenson 2005), which had returned to breed at its natal colony. Gender of these banded individuals was ascertained from DNA samples following Daniel et al. (2007). The 3.5-g loggers (<0.2% of adult body weight) were attached with two cable ties to darvic PVC plastic leg bands (Rayner et al. 2008), and retrieved from birds A08, A77, and B60 early in the subsequent breeding season. All three birds subsequently bred in the 2008-2009 season. Birds M-74768 and M-74777 also returned to the Cape Kidnappers Plateau colony to breed in 2008, but had lost the GLS devices from the plastic bands.

Geolocator data from the three retrieved devices were processed following Phillips et al. (2004). Times of sunrise and sunset were estimated from light records, and converted to location estimates using TransEdit and BirdTracker software (British Antarctic Survey, Cambridge, UK). Transitions associated with poor quality light curves were identified during processing, and the resulting positions were excluded, as appropriate, after visualization in a GIS. Only longitudes were available around equinoxes, when daylength is similar throughout the world. The primary areas frequented by tracked birds were mapped as kernel density plots with the Spatial Analyst extension of ArcMap 9.3 (ESRI Inc. 1999) applying an ITRF 2005 geographic coordinate system (Fig. 1). Density contours were set to display the top 80% of spatial use around the Cape Kidnappers Gannetry, New Zealand, and at Australian wintering areas. A conservative estimate of the distances covered during migration was calculated for each bird, based on core areas of the kernel estimates (Cape Kidnappers Gannetry, New Zealand; and top 20% of the kernel densities on the Australian/Tasmanian coast) with minimum distances between landmarks calculated, assuming direct travel over water. Estimated migration paths between breeding and wintering areas were plotted for orientation, but should be treated as approximations, given the typical measurement errors of ~186–202 km recorded

FIG. 1. Migration routes of (A) a male and (B) a female adult Australasian Gannets (Morus serrator), and (C) a male hybrid between M. serrator and M. capensis between breeding seasons 2007-2008 and 2008-2009 at Cape Kidnappers Gannetry, New Zealand; colored symbols: highest quality positions obtained using geolocators; dashed lines: approximate migration routes inferred, lines darker with advancing time.
FIG. 2. Time of year over weekly means of longitude during the non-breeding period for three adult gannets equipped with geolocators at Cape Kidnappers Plateau Colony; A08 male Australasian Gannet, A77 female Australasian Gannet, B60 male Cape Gannet × Australasian Gannet.

RESULTS

Both Australasian Gannets and the *M. capensis* × *M. serrator* hybrid migrated across the Tasman Sea, spending between 2 (hybrid B60) and 4 months (Australasian Gannets A08 and A77) in Australian and Tasmanian coastal waters (Fig. 2) before returning to the same subcolony at Cape Kidnappers (Fig. 1). These wintering areas were straight-line distances of 3,450 km (A08) and 2,350 km (A77 and B60) from the gannetry. Distances covered during migration between breeding seasons were at least 13,000 km for A08 (Fig. 1A), 5,800 km for A77 (Fig. 1B), and 10,000 km for B60 (Fig. 1C).

The male Australasian Gannet A08 (Fig. 1A) passed the North Cape (176.48° E, 32.66° S) on 13 March 2008 and subsequently crossed the Tasman Sea to reach Bass Strait (147.73° E, 40.07° S) on 15 April 2008, from where it continued to the area of Kangaroo Island, South Australia, in the Great Australian Bight (139.79° E, 38.24° S; 22 Apr 2008). This bird spent 93 days in this region, before it passed Bass Strait again on 24 July 2008. A08 appeared to follow the Australian East Coast somewhat northward (153.97° E, 34.71° S on 14 Aug 2008) before it crossed the Tasman Sea again and reached Cook Strait (174.77° E, 40.88° S) on 21 August 2008. The bird subsequently left New Zealand waters a second time to fly to the East Australian Coast (154.06° E, 28.29° S; 28 Aug 2008), via North Cape New Zealand (174.39° E, 35.20° S; 21 Aug 2008). It followed the Australian coastline south to Bass Strait (150.35° E, 42.76° S; 30 Aug 2008), and flew across the Tasman Sea taking a route via Stewart Island (167.16° E, 50.1° S; 08 Sep 2008) to its breeding location. This second trip across
the Tasman Sea to Australian coastal waters and back to the New Zealand gannetry was completed in 21 days, covering a minimum distance of 6,900 km.

The female Australasian Gannet A77 (Fig. 1B) appeared to use Cook Strait (173.72° E, 40.70° S; 1 Apr 2008) to cross the Tasman Sea towards Bass Strait (150.11° E, 39.41° S; 7 Apr 2008). Its wintering areas extended from Bass Strait both south of Tasmania (146.55° E, 44.95° S) and north along the Australian East Coast (150.88° E, 34.82° S), from where it crossed the Tasman Sea again after 119 days, and reached the Cape Kidnappers Gannetry via Stewart Island and West Cape, and the East Coast of the South and the North islands New Zealand (167.87° E, 46.97° S; 16 Aug 2008). It subsequently left Cape Kidnappers again for 23 days for the regions further north along the New Zealand East Coast, off the Bay of Plenty and the Bay of Islands. This female returned via the East Cape (178.79° E, 36.85° S; 22 Oct 2008) to its Cape Kidnappers breeding areas.

The hybrid male B60 (Fig. 1C) started its migration from the region of the Bay of Plenty (179.03° E, 37.40° S) on 8 April 2008, circumvented the North Cape (176.35° E, 34.58° S) on 11 April 2008, and appeared to follow the New Zealand west coast southward before starting its cross-Tasman flight from West Cape (167.43° E, 48.54° S) on 15 April 2008. B60 stayed 59 days (21 Apr 2008–19 Jun 2008) in and around its wintering areas as defined by the highest 80% kernel density, which resembled that of A77. B60 spent 9 days in the region of the Lord Howe Islands (160.39° E, 34.90° S; 25 Jun 2008) on its flight across the Tasman Sea back to New Zealand, before it was tracked to waters north of North Cape (172.29° E, 33.12° S) on 7 July 2008. B60 consequently returned for 11 days to mid Tasman Sea waters (164.89° E, 36.25° S), before reaching the Cape Kidnappers breeding area again via the North Cape (176.42° E, 35.76° S; 25 Aug 2009) and the Bay of Plenty (179.12° E, 33.14° S; 27 Aug 2008).

Longitudinal movements of the three birds varied (Fig. 2). These birds spent 180, 208, and 142 days, respectively, away from the colony before their final return to the breeding site.

**DISCUSSION**

We provide the first direct evidence that both male and female adult Australasian Gannets migrate from New Zealand breeding areas to winter in Australian waters. A hybrid (Cape X Australasian Gannet, Robertson and Stephenson 2005) also displayed the same general pattern. Our study is suggestive of a high level of individual variability in routes, timing of arrival and departure, and duration and destination, suggesting considerable plasticity in migration behavior. Our findings indicate the importance of the Bay of Plenty and Bay of Islands north of the gannetry on the east New Zealand coast, which were frequented by all three tracked birds before departure on their trans-Tasman flights, or upon return to New Zealand prior to breeding. All three potential migration routes around New Zealand landmasses between Cape Kidnappers and the Tasman Sea (i.e., North Cape, Cook Strait, and Stewart Island) were used. One bird (B60) appeared to forage extensively in the open waters of the Tasman Sea. However, sample sizes were small and further studies are required. Our results suggest adult migration behavior is more variable than that of fledglings, which appear to minimize time spent in flight and distance traveled over the open ocean (Ismar et al. 2010b). There may be less pressure on adults to travel directly because of their higher foraging efficiency (Nelson 1978).

The female Australasian Gannet covered the shortest distance during migration, and spent the longest time away from the gannery. This fits with a male accrued task of territorial establishment in the early breeding season, as found in the congeneric Northern Gannet (Nelson 2002). Thus, males should be more constrained in foraging ranges than females at this time of year. Asynchronous arrival at the breeding site by males and females is also suggested for M. serrator (Ismar et al. 2010a). Further research is needed to gain sufficient sample sizes to fully investigate differences in migration between male and female Australasian Gannets, and to compare migratory pathways and dynamics with birds from other New Zealand and Australian breeding locations.

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Office, kindly provided accommodation in the field, and Cape Kidnappers landowners and farm managers kindly gave admission to the property. We thank Michael G. Anderson, Sandra H. Anderson, Donald C. Dearborn, Andrea Gager, Jethro S. Johnson, Angela F. Little, Gabriel Machovský-Capuská, Craig D. Millar, Mala Nesaratnam, Stuart Parsons, David Raubenheimer, Rachel C. Shaw, Vivian Ward, Sarah J. Withers for help in the field, and Scott A. Shaffer and an anonymous referee for constructive comments on the manuscript.

LITERATURE CITED


BIRDS CONSUMED BY THE INVASIVE BURMESE PYTHON (*PYTHON MOLURUS BIVITTATUS*) IN EVERGLADES NATIONAL PARK, FLORIDA, USA

CARLA J. DOVE,¹ ⁴ RAY W. SNOW,² MICHAEL R. ROCHFORD,³ AND FRANK J. MAZZOTTI³

ABSTRACT.—We identified 25 species of birds representing nine avian Orders from remains in digestive tracts of 85 Burmese pythons (*Python molurus bivittatus*) collected in Everglades National Park, Florida, USA, from 2003 to 2008. Four species of birds identified in this study are of special concern in Florida and a fifth, the Wood Stork (*Mycteria americana*), is listed as federally endangered. This represents the first detailed analysis of the avian component of the diet of the introduced Burmese python, now established in Everglades National Park, Florida and highlights the potential for considerable negative impact of this invasive species on native bird populations. Received 9 June 2010. Accepted 21 September 2010.

The Burmese python (*Python molurus bivittatus*) is now well established in Everglades National Park (ENP), Florida (Snow 2006, Snow et al. 2007c). These snakes, often considered a subspecies of the Indian python (*P. molurus*), can grow to 6 m and weigh 90 kg (Ernst and Zug 1996). The Burmese python was first recorded in the Everglades in 1979 and has since frequently been observed or collected in canals, along main park roads, and even in remote mangrove (red mangrove, *Rhizophora mangle*; black mangrove, *Avicennia germinans*; white mangrove, *Laguncularia racemosa*; buttonwood, *Conocarpus erecta*) backcountry areas (Snow et al. 2007a). Large specimens of this snake were reported in ENP in the 1980s (Meshaka et al. 2000) but have only been documented as breeding in the United States since 2006 (Snow et al. 2007b). The Burmese python has spread throughout ENP over the past two decades and has also been recorded in the Florida Keys and elsewhere in Florida.

Typical food items consumed by the closely related Indian python (*P. molurus molurus*) include mammals, amphibians, lizards, snakes, birds, and fish (Ernst and Zug 1996). Researchers are just now beginning to investigate the dietary habits of the Burmese python in ENP to help identify the impact of this invasive species on the native fauna (Snow et al. 2007a). Mammal species recorded as prey by the Burmese python in ENP include rodents and carnivores (Snow et al. 2007a), and as reported by Greene et al. (2007), the endangered Key Largo woodrat (*Neotoma floridana smalli*).

We identified birds consumed by Burmese pythons in ENP from 2003 to 2008 using a combination of feather identification techniques and morphological comparisons of osteological fragments. Many of the same samples examined were used to identify mammalian prey (Snow et al. 2007a). Continued documentation of the prey species of this invasive snake will add to our knowledge of the diet of the Burmese python in ENP, and alert conservation agencies, park officials, and the pet trade of the potential devastation this species can cause to native bird populations that did not evolve with this type of predator.

METHODS

Eighty-five of 343 Burmese pythons (25%) collected within Everglades National Park locations (Fig. 1) during 2003–2008 were found to have bird remains in the intestinal tracts. Standard mass (g) and measurements (cm) of total length and snout-vent length were available for most of the pythons examined.

Intestinal tracts or gut contents of individual Burmese pythons were sent to the Feather Identification Laboratory, National Museum of Natural History, Smithsonian Institution, in Washington, D.C. for bird species identification. Identification of species of birds from fragmentary feathers has frequently been applied to ecological studies of prey remains (Day 1966, Gilbert and Nancekivell 1982, Griffin 1982, Ward

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FIG. 1. Everglades National Park, Florida and surrounding area showing collection sites of Burmese pythons examined in this study (Map by M. R. Rochford).
TABLE 1. Size and mass (± SD) of Burmese pythons that were feeding on birds and collected in Everglades National Park, Florida, USA (2003–2008). Range data for all measurements are estimated to the nearest decimal point.

<table>
<thead>
<tr>
<th></th>
<th>Total length (cm)</th>
<th>Snout-vent length (cm)</th>
<th>Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td></td>
<td>n</td>
</tr>
<tr>
<td>Male</td>
<td>231.8 ± 52.6; range 91–325</td>
<td>202.1 ± 45.7; range 80–286</td>
<td>6,415 ± 3,524; range 990–17,054</td>
</tr>
<tr>
<td>Female</td>
<td>276.0 ± 72.4; range 114–475</td>
<td>243.7 ± 65.2; range 99–424</td>
<td>12,158 ± 11,778; range 490–56,690</td>
</tr>
<tr>
<td>Totals</td>
<td>255.8 ± 67.4; range 91–475</td>
<td>224.7 ± 60.5; range 80–424</td>
<td>9,508 ± 9,371; range 490–56,690</td>
</tr>
</tbody>
</table>

and Laybourne 1985) when ample material is available. Python gut samples were first sorted and cleaned following methods used by Sabo and Laybourne (1994) for dry pellets. Many of these samples were wet or frozen and often odoriferous. Thus, we worked in a fume hood to sort and conduct initial cleaning. Species identification methods used depended on the type, quality, and quantity of material, and on the extent of digestion of each sample. Large items of whole feathers, feather fragments, or partial bones were subsampled and cleaned separately. This reduced the amount of time in the cleaning process and left some material with the original sample for future analysis of other food items.

Microscope slides were made from downy feather barbules in gut samples following Dove et al. (2005) for fragmentary evidence. The feather identification technique involved examining the variation in the microscopic characters of the plumulaceous (downy) barbs and comparison of whole feathers or large pieces of feathers to museum study skins stored in the Division of Birds, National Museum of Natural History. Microscopic identifications were primarily used to identify the material to taxonomic Order or Family (i.e., Rallidae, Anatidae) of each sample, and then in combination with other feather fragments, osteological material, geographic location, and circumstantial evidence associated with the sample to corroborate species identifications. We counted samples that contained more than one species of bird (e.g., sample #128; Anatidae and Anhingidae) accordingly but were unable to ascertain if more than one individual of the same species was consumed in heavily digested samples. We used measurements of ~260 cm TL for females and ~200 cm TL for males provided by Reed and Rodda (2009), to ascertain if pythons were mature.

RESULTS

Gender, length, and mass were available for most pythons examined. The ratio of males to females was nearly equal (37 males, 44 females). Males were smaller than females in both mass and body measurements (Table 1). Sixty-eight of the 85 Burmese pythons in this study were ascertained to be mature based on measurements. Burmese pythons were collected throughout ENP during every month of the year with most being collected in December and January.

We identified 25 species of birds representing nine avian Orders from the 85 Burmese pythons (Table 2). Eighty-nine individual birds were recorded including 54 that were identified to species level, one identified to Order, 18 identified to Family, and 16 that were identified only as Aves (bird), due to lack of diagnostic feather material. Gruiformes (rails and allies) were the most numerous bird prey of Burmese pythons and represented eight species and 32 individuals (36% of birds consumed). Ciconiiformes (herons and bitterns) were also common in the samples (18%) and included six of the 13 species occurring in Florida. Pied-billed Grebe (Podilymbus podiceps), White Ibis (Eudocimus albus), and Limpkin (Aramus guarauna) were the species most commonly identified, each occurring in seven different python samples. The most interesting prey item encountered was a Magnificent Frigatebird (Fregata magnificens; sample #744) collected ~50 km from a known roosting area for frigatebirds (R. W. Snow, pers. obs.). Domestic Chicken (Gallus gallus domesticus) was found in two separate samples and Domestic Duck (Anas platyrhynchos domesticus) in one sample collected near agricultural areas that abut the park. Four species identified, Little Blue Heron (Egretta caerulea), Snowy Egret (E. thula), White Ibis, and Limpkin are considered species of special concern by the Florida Fish and Wildlife Conservation Commission (Gruver 2010) and a fifth, the Wood Stork (Mycteria americana), is listed as federally endangered (Federal Register: 27 September 2006, Volume 71, Number 187). We found no evidence of eggs or chicks in any of the python samples examined.
TABLE 2. Eighty-nine individual birds representing nine avian Orders and 25 species consumed by Burmese pythons in Everglades National Park, Florida, USA. Birds were identified in 25% of the 343 pythons collected during 2003-2008. Python field numbers shown in bold indicate multiple bird species consumed by one snake. Numbers in parentheses = % of Order in diet rounded to nearest decimal point.

<table>
<thead>
<tr>
<th>Order</th>
<th>Species</th>
<th>Number of individual birds</th>
<th>Python field number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Podicipediformes</td>
<td>Pied-billed Grebe (<em>Podilymbus podiceps</em>)</td>
<td>7</td>
<td>104,124,202,339,364,740,846</td>
</tr>
<tr>
<td></td>
<td>Podicipedidae (unidentified species)</td>
<td>1</td>
<td>504</td>
</tr>
<tr>
<td>Pelicaniformes</td>
<td>Magnificent Frigatebird (<em>Fregata magnificens</em>)</td>
<td>2</td>
<td>128,844</td>
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<tr>
<td></td>
<td>Anhinga (<em>Anhinga anhinga</em>)</td>
<td>1</td>
<td>547</td>
</tr>
<tr>
<td></td>
<td>Great Blue Heron (<em>Ardea herodias</em>)</td>
<td>1</td>
<td>491</td>
</tr>
<tr>
<td></td>
<td>Snowy Egret (<em>Egretta thula</em>)</td>
<td>1</td>
<td>484</td>
</tr>
<tr>
<td></td>
<td>Little Blue Heron (<em>E. caerulea</em>)</td>
<td>1</td>
<td>327</td>
</tr>
<tr>
<td></td>
<td>White Ibis (<em>Eudocimus albus</em>)</td>
<td>7</td>
<td>113,168,492,580,760,887,918</td>
</tr>
<tr>
<td></td>
<td>Wood Stork (<em>Mycteria americana</em>)</td>
<td>1</td>
<td>539</td>
</tr>
<tr>
<td></td>
<td>Ardeidae (unidentified species)</td>
<td>2</td>
<td>503,552</td>
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<tr>
<td></td>
<td>Threskiornithidae (unidentified species)</td>
<td>1</td>
<td>177,804</td>
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<tr>
<td>Anseriformes</td>
<td>Northern Pintail (<em>Anas acuta</em>)</td>
<td>1</td>
<td>1141</td>
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<tr>
<td></td>
<td>Blue-winged Teal (<em>A. discors</em>)</td>
<td>1</td>
<td>310</td>
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<tr>
<td>Galliformes</td>
<td>Domestic Duck (<em>A. platyrhynchos domesticus</em>)</td>
<td>3</td>
<td>128,513,870</td>
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<td></td>
<td>Anatidae (unidentified species)</td>
<td>1</td>
<td>653,731</td>
</tr>
<tr>
<td></td>
<td>Domestic Chicken (<em>Gallus gallus domesticus</em>)</td>
<td>2</td>
<td>509,1158</td>
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<tr>
<td>Charadriiformes</td>
<td>Purple Gallinule (<em>Porphyrio martinica</em>)</td>
<td>2</td>
<td>451</td>
</tr>
<tr>
<td></td>
<td>Common Moorhen (<em>Gallinula chloropus</em>)</td>
<td>3</td>
<td>325,546,553</td>
</tr>
<tr>
<td></td>
<td>American Coot (<em>Fulica americana</em>)</td>
<td>2</td>
<td>379,781</td>
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<td>Clapper Rail (<em>Rallus longirostris</em>)</td>
<td>4</td>
<td>242,362,437,478</td>
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<td></td>
<td>Virginia Rail (<em>R. limicola</em>)</td>
<td>1</td>
<td>163</td>
</tr>
<tr>
<td></td>
<td>Sora (<em>Porzana carolina</em>)</td>
<td>2</td>
<td>500,535</td>
</tr>
<tr>
<td></td>
<td>Limpkin (<em>Aramus guarauna</em>)</td>
<td>7</td>
<td>129,363,373,460,507,514,551</td>
</tr>
<tr>
<td></td>
<td>Rallidae (unidentified species)</td>
<td>10</td>
<td>120,196,316,341,369,512,549,567,568,754</td>
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<tr>
<td>Columbiformes</td>
<td>Whimbrel (<em>Numenius phaeopus</em>)</td>
<td>1</td>
<td>451</td>
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<tr>
<td></td>
<td>Columbidae (species unidentified)</td>
<td>1</td>
<td>653</td>
</tr>
<tr>
<td></td>
<td>House Wren (<em>Troglodytes aedon</em>)</td>
<td>1</td>
<td>77</td>
</tr>
<tr>
<td></td>
<td>Red-winged Blackbird (<em>Agelaius phoeniceus</em>)</td>
<td>1</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>Eastern Meadowlark (<em>Sturnella magna</em>)</td>
<td>1</td>
<td>603</td>
</tr>
<tr>
<td></td>
<td>Passerine (unidentified species)</td>
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<td>491</td>
</tr>
<tr>
<td>Passeriformes</td>
<td>Aves (unidentified species)</td>
<td>16</td>
<td>283,374,469,508,510,515,519,528,538,555,561,563,727,756,854,871</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>89</td>
<td>85</td>
</tr>
</tbody>
</table>

DISCUSSION

Identification of prey remains from fragmentary evidence is vital to help document the diets of invasive predators. Our analysis demonstrates that even if the dietary material was heavily digested and in poor condition, we were able to provide species-level identifications for many of the samples. Most species-level identifications were based on the presence of whole feathers or large fragments of feathers and bone which allowed exact morphological comparison. This allows high confidence in the species-level identifications, and microscopic analysis allowed us to obtain Family-level identification of gut samples that did not contain sufficient macroscopic material for whole feather/bone comparison. Seventeen of the samples noted as heavily digested contained large portions of avian feet, partial bills and skulls that assisted greatly with species identifications; these anatomical parts apparently are the last to be processed within the pythons' digestive system.

The Rallidae (rails and allies) was the group most heavily consumed by Burmese pythons in ENP. The threat of this unfamiliar predator to rails
and other birds is eminent. The seven species of rails identified occupy habitats in ENP that are familiar to the Burmese python and include both freshwater and brackish marshes, riverbanks, mud flats, and areas of dense vegetation. Rails have been particularly vulnerable throughout history to extinction on islands, mainly from introduced predators. The extinction of the Guam Rail (Gallirallus owstoni) was the first documented case of a snake (brown tree snake, Boiga irregularis) being implicated as an agent of extinction (Taylor 1996). Limpkin were recorded in nearly 8% of the samples analyzed. This species typically nests in Florida from February through June, roosts in trees or shrubs at night, and forages nocturnally year-round (Bryan 1996) making it particularly vulnerable to predation by the Burmese python. This python in ENP is noted as being nocturnal during June–August and mainly diurnal in October–April (R. W. Snow, pers. obs.), the closely related Indian python is active both day and night (Zug and Ernst 2004).

The dietary habits of invasive pythons are broad and represent a threat to the native fauna of the diverse habitats that it is capable of inhabiting. Ground-dwelling birds such as rails and egrets are particularly threatened because not only are they susceptible to predation of eggs and young by resident carnivores and birds, but the adult age cohort has a newly established effective predator. The high reproductive rate, longevity, ability to consume large prey (Rodda et al. 2009), and foraging strategies of avian species by pythons, is cause for serious conservation, educational, and eradication measures. This predator is particularly hazardous to native bird populations in North America because birds have not evolved in conjunction with a large predator that has both diurnal and nocturnal feeding habits and is capable of consuming large and small prey items. Despite continuing discussions over the potential northward spread of these pythons by Rodda et al. (2009) and Pyron et al. (2008), Federal species recovery plans should seriously consider and address this novel threat in future plans.

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INTERBREEDING OF *AECHMOPHORUS* GREBES
ANDRÉ KONTER

ABSTRACT.—I analyzed the occurrence of intermediates between Western (*Aechmophorus occidentalis*) and Clark's (*A. clarkii*) grebes, of mixed pairings, and of species composition in populations of *Aechmophorus* grebes in California and Oregon, USA. Western Grebes comprised 69% of the aggregated total of grebes identified while intermediates represented ~3.5% (41-46 individuals) in the populations investigated. I conclude that numbers of intermediates between purebred parental individuals have increased. Higher percentages of mixed pairings were observed at Lake Almanor; an aggregated 7.9% of nesting pairs were not composed of two purebred grebes of the same species. Statistically, mating remained strongly assortative. Received 1 June 2010. Accepted 22 September 2010.

The American Ornithologists' Union split the two North American *Aechmophorus* grebes in 1985 into Western (*A. occidentalis*) and Clark's (*A. clarkii*) grebes (AOU 1985). Both arose from a common ancestral population that divided into northern and southern subpopulations; differences between both developed during a period of geographical isolation (Storer and Nuechterlein 1985). More recently the ranges of both have become largely sympatric and differences in their advertising calls were identified as critical to their reproductive isolation (Nuechterlein 1981b).

Genetic investigations suggest the taxonomy of *Aechmophorus* grebes might not be entirely settled (Ahlquist et al. 1987, Bledsoe and Sheldon 1989, Guerra and Speed 1996, Hebert et al. 2003, Savolainen et al. 2005, Ratnasingham and Hebert 2007). However, genetically low levels of differentiation cannot be used alone to establish species boundaries as they reflect the time of divergence of lineages (Ahlquist et al. 1987). A crucial question to be answered in the field is whether barriers to random mating between Western and Clark's grebes are increasing or vanishing.

My objectives were to investigate: (1) mixed pairings of *Aechmophorus* grebes, (2) the occurrence of intermediates, and (3) the proportions of Clark's and Western grebes at different locations in northern California and southern Oregon, USA.

**METHODS**

*Study Sites.*—Sites visited during the study and having grebes were Upper Klamath Lake, Lake Ewauna and Drews Reservoir, all in Oregon, Tule Lake National Wildlife Refuge (NWR), Lake Almanor, Lake Shastina, East Park Reservoir, all in California, and Goose Lake, straddling both states. Water surfaces, elevations, and geographical coordinates of study sites varied (Table 1). An additional survey was made along the Pacific Coast, south of Fort Ross, California when I unexpectedly encountered a group of *Aechmophorus* grebes at sea on 7 August 2009.

*Timing and Recording of Data.*—Study sites were visited for 12 days between 25 July and 5 August 2009. Three different areas were screened for grebes at Upper Klamath Lake: Moore Park and the Marina, Wocus Bay, and Eagle Ridge. Two screens were made at Lake Ewauna from Timber Mill Shores. Few grebes were observed at Goose Lake due to low water levels and the site was not further explored. Tule Lake NWR was visited by driving along the shore on two access roads. Each time grebes were encountered, I stopped to identify them. Two grebe colonies were present in the northwest part of Lake Almanor. Observations there occurred from the shore. East Park Reservoir was screened at four different access points. Low water levels at Lake Shastina permitted access by walking to a small island from where data were recorded.

*Aechmophorus* grebes present were counted with the help of 10 × 25 Zeiss binoculars. All grebes sufficiently close for species identification were scanned using a Konica Minolta Dynax 7D camera with a Sigma AF 800 mm auto focus lens mounted on a tripod. After identification, the species (Western, Clark's, or intermediate grebes) was registered by an assistant. The composition of all pairs encountered was also recorded. Photos were immediately taken of each intermediate, of each grebe with a doubt about a pure-bred species status, of mixed pairs, and of pairs comprising individuals with uncertain species status. Species status for nesting pairs at Lake Almanor was assessed per nest platform. Species status was also recorded for displaying pairs. Species distribution
and composition at each location was estimated based on identification from all samples. A $\chi^2$-test using the VassarStats web site for statistical computation was applied to test if pairing by the grebes was random or assortative with respect to species.

Identification of Grebe Species (Western vs. Clark’s).—Species identification of exclusively adults followed the descriptions provided by Storer and Nuechterlein (1985) and their subdivision of diverging areas of the face between Western and Clark’s grebes into lores, above eye, behind eye, and below eye (Storer and Nuechterlein 1985: 103, fig. 1) complemented by descriptions in Ratti (1981), Eichorst and Parkin (1991), and Konter (2009). Little intermedicy and no overlap between both species is to be found in adults during the breeding season from April to October.

Individuals were classified as Clark’s Grebes if they had an orange-yellow bill with a sharply defined black culmen, white lores and white feathers above, behind, and below the eye so the black crown ended clearly above the eye. Individuals were classified as Western Grebes if they had a dull yellow-green bill and the black of the crown extended to below the eyes. All grebes not entirely conforming to the descriptions of purebred Western or Clark’s grebes were a priori classified as intermediates, unless divergence was minimal, in which case they were classified as ±Western or ±Clark’s grebes. The term “intermediate” as applied here is not limited to first generation hybrids, but may include backcrosses.

RESULTS

Numbers and species composition of populations observed varied (Table 2). Not considering possible intermediates, I found an aggregated 69% of Western Grebes, which represented the majority of the grebes at Tule Lake NWR, Lake Almanor and, to a lesser extent, Lake Shastina. Western Grebes were present over three times as often as Clark’s Grebes in the group seen along the Pacific Coast.

Forty-one grebes were classified as intermediates between Clark’s and Western grebes. Another five differed only slightly from purebred grebes and their status was unclear. Intermediates represented between 0.6% (Tule Lake NWR) and 4.4–6.6% (East Park Reservoir) of local populations, or an aggregated 3.3–3.7% of all grebes identified in this study (Table 2).

Most grebes at Lake Almanor were nesting and no pairs tending young were found. Several pairs were building on rather recent platforms and others searched the colony for a nesting space. Some individuals were still engaged in water courtship. The owners for 267 platforms could be identified: 246 were occupied by purebred pairs composed of either two Western ($n = 197$, 80.1%) or two Clark’s grebes ($n = 29$, 12.0%). Four pairs (1.5%) were mixed, composed of one Western and one Clark’s grebe. Nine of the observed intermediates (3.4%), were paired with partners that remained unidentified, another seven (2.6%) were paired to purebred Western ($n = 4$) or Clark’s grebes ($n = 3$), and one pair (0.4%) was composed of two intermediates. Thus, 7.9% of the aggregated nesting pairs were not composed of two purebred grebes of the same species. This percentage was 27.8% ($n = 5$) for 18 displaying pairs: one pair was composed of two intermediates, two additional intermediates displayed with two Western Grebes, and two pairs were composed of one Western and one Clark’s Grebe.
### TABLE 2. Adult Clark’s (CG), Western (WG), and intermediate grebes (IG, ±CG, ±WG) in surveys and proportions of pure and intermediate grebes by survey site.

<table>
<thead>
<tr>
<th>Location</th>
<th>CG</th>
<th>WG</th>
<th>IG ±CG</th>
<th>±WG</th>
<th>Total population</th>
<th>% CG-WG</th>
<th>% IG, ±CG, ±WG</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Park Reservoir</td>
<td>60</td>
<td>25</td>
<td>4</td>
<td>1</td>
<td>94</td>
<td>66-27%</td>
<td>4.4-6.6%</td>
</tr>
<tr>
<td>Drews Reservoir</td>
<td>4</td>
<td>2</td>
<td>12</td>
<td>1</td>
<td>~30</td>
<td>67-33%</td>
<td>c</td>
</tr>
<tr>
<td>Upper Klamath Lake</td>
<td>143</td>
<td>123</td>
<td>12</td>
<td>1</td>
<td>~350</td>
<td>51-44%</td>
<td>4.3-4.7%</td>
</tr>
<tr>
<td>Lake Ewauna</td>
<td>48</td>
<td>21</td>
<td>1</td>
<td></td>
<td>90</td>
<td>70-30%</td>
<td>0</td>
</tr>
<tr>
<td>Tule Lake NWR</td>
<td>3</td>
<td>158</td>
<td>1</td>
<td></td>
<td>~180</td>
<td>2-97%</td>
<td>0.6%</td>
</tr>
<tr>
<td>Lake Shastina</td>
<td>52</td>
<td>39</td>
<td>1</td>
<td></td>
<td>225</td>
<td>46-53%</td>
<td>0.9%</td>
</tr>
<tr>
<td>Lake Almanor</td>
<td>77</td>
<td>462</td>
<td>23</td>
<td>1</td>
<td>2,112</td>
<td>14-82%</td>
<td>4.1-4.3%</td>
</tr>
<tr>
<td>Totals</td>
<td>387</td>
<td>850</td>
<td>41</td>
<td>2</td>
<td>3,081</td>
<td>31-69%</td>
<td>3.3-3.7%</td>
</tr>
<tr>
<td>Pacific Coast b</td>
<td>19</td>
<td>64</td>
<td></td>
<td></td>
<td>170</td>
<td>23-77%</td>
<td></td>
</tr>
</tbody>
</table>

* Total population counted in areas surveyed.

b Birds were too far out for identifying intermediates.

c Few grebes could be correctly identified at Drews Reservoir.

The composition of observed pairings with known partners was strongly assortative \( (\chi^2 = 236.49, \text{df} = 5, P < 0.0001) \) at Lake Almanor. This did not change if the nine intermediates with unknown partners were included, assuming an expected distribution of the partner’s species status \( (\chi^2 = 230.13, \text{df} = 5, P < 0.0001, \) Table 3). No historical data about mixed pairings could be found for Lake Almanor. All pairs tending young at Tule Lake NWR were composed of purebred Western Grebes \( (n = 34) \).

### DISCUSSION

My study confirms strongly assortative mating between the two *Aechmophorus* species although, at Lake Almanor, the percentage of nesting pairs not composed of two purebred grebes of the same species \( (7.9\%) \) largely exceeds those found in earlier studies in California and Oregon. For instance, Ratti \( (1979) \) recorded one mixed pair \( (2.8\%, n = 36) \) in 1977 at Upper Klamath Lake and none at Tule Lake NWR \( (n = 139) \). Nuechterlein \( (1981a) \) observed only one mixed pair at Upper Klamath Lake in 1979, too. He found mixed pairs represented 3% of male-female courtship displays at Tule Lake NWR, but only 1.1% in breeding pairs \( (n = 91) \) in 1979. Ratti \( (1979) \), in over 600 independent observations of pairs in California and Oregon, found that mixed pairs represented 1.2% of pre-nesting pairs and 0.25% \( (n = 766) \) of pairs with young. Lindvall and Low \( (1982) \), in other areas of sympathy, observed 0.6% \( (n = 161; 1974) \), Ratti \( (1979) \) 1.9% \( (n = 719; 1975) \) and 0.8% of mixed pairs \( (n = 566; 1976) \) at Bear River Migratory Bird Refuge. Ratti \( (1979) \) calculated that 1.2% of 1,185 pairs observed in 1975-1977 for all of Utah represented mixed pairs.

The current study found increased numbers of intermediates representing \( \sim3.5\% \) in the popula-

### TABLE 3. Observed and expected frequencies of pairings (nesting and displaying birds) among Western \( (n = 462) \), Clark’s \( (n = 77) \), and intermediate grebes \( (n = 24) \), not considering the nine nesting intermediates with unknown partner and assuming a random distribution of their partners \( (i.e., 7 \text{ Western, 1 Clark’s, and 1 intermediate}) \) reflecting the composition of the population.

<table>
<thead>
<tr>
<th>Pair composition</th>
<th>Without nine intermediates with unknown partners</th>
<th>With random distribution of the nine intermediates’ partners</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed frequency</td>
<td>Expected frequency</td>
</tr>
<tr>
<td>WGxWG</td>
<td>225</td>
<td>186</td>
</tr>
<tr>
<td>WGxCG</td>
<td>6</td>
<td>62</td>
</tr>
<tr>
<td>WGxIG</td>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td>CGxCG</td>
<td>34</td>
<td>5</td>
</tr>
<tr>
<td>CGxIG</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>IGxIG</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

\( \chi^2 \) Goodness of fit test \( \chi^2 = 236.49, \text{df} = 5, P < 0.0001 \) \( \chi^2 = 230.13, \text{df} = 5, P < 0.0001 \)
numbers of pairs not composed of two purebred Parent species (Mayr 1951, Bigelow 1965, Ratti recent data exist for comparison. (15) at Laguna total population of 105 and 30% (n = 54) at Laguna Tuxpan with a %{n = represented 51 nd, in surveys by Feerer (1977), intermediates a Grebes, seem to show a completely different picture populations, generally dominated by Clark's grebes of the same species and the increased levels of hybridization in sympatric and allopatric These numbers are in the range of those found Manitoba and Saskatchewan (Konter 2009). ed <4% of the breeding population at Delta Marsh, Manitoba, around 1980 and in the early 1990s (Nuechterlein and Buitron 1998) and, in 2008, they comprised ~3% on different lakes in Manitoba and Saskatchewan (Konter 2009). These numbers are in the range of those found in this study and a priori indicate comparable levels of hybridization in sympatric and allopatric populations. It is also noteworthy that Mexican populations, generally dominated by Clark's Grebes, seem to show a completely different picture and, in surveys by Feerer (1977), intermediates represented <4% of the breeding population at Delta Marsh, Manitoba, around 1980 and in the early 1990s (Nuechterlein and Buitron 1998) and, in 2008, they comprised ~3% on different lakes in Manitoba and Saskatchewan (Konter 2009). We should expect Aechmophorus grebes to hybridize to a lesser extent in regions of sympathy than in regions of relative allopatry (based on Randler 2006), such as prairie Canada with only 1-4% of Clark's Grebes. Intermediates represented <4% of the breeding population at Delta Marsh, Manitoba, around 1980 and in the early 1990s (Nuechterlein and Buitron 1998). Unfortunately, no recent data exist for comparison. Speciation is regarded as essentially complete if, during sympatry, interbreeding is reduced to a level that prevents genetic swamping by the parent species (Mayr 1951, Bigelow 1965, Ratti 1979). We may question whether the high numbers of pairs not composed of two purebred grebes of the same species and the increased percentages of intermediates found here are sufficient to prevent both Aechmophorus species from merging. We also have to consider that the numbers of all-generation intermediates recorded in the field may be biased by their detection rate (Randler 2004) and, that by introgressive hybridization (Anderson and Hubricht 1938), they are absorbed into one of the parental species. Later generation hybrids are likely cryptic and similar to the dominant parental type. The resulting asymmetric introgression could perhaps best be assessed by analyzing shifts in the composition of the combined Aechmophorus populations, although causes other than hybridization may alter the relative abundance of both species. Complete counts have only been introduced more recently in California and Oregon in the context of declining global grebe populations following breeding and wintering habitat loss or degradation (e.g., consequences of oil spills, eutrophication, and water level fluctuations at breeding sites) and conflict with leisure activities. The data do not permit assessing historical developments in this respect as species composition was only analyzed to a limited extent. Aechmophorus grebes at the current levels of intermediates and assortative mating still provide sufficient confidence for conferring species status to both. Developments should be closely monitored as mate choice may break down when the population consists almost entirely of highly recombined hybrids (Barton and Hewitt 1985).

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NESTING BIOLOGY, HOME RANGE, AND HABITAT USE OF THE BROWN WOOD RAIL (ARAMIDES WOLFI) IN NORTHWEST ECUADOR

JORDAN KARUBIAN,1,4 LUIS CARRASCO,2 PATRICIO MENA,2 JORGE OLIVO,2 DOMINGO CABRERA,2 FERNANDO CASTILLO,2 RENATA DURAES,1 AND NORY EL KSABI3

ABSTRACT.—The Brown Wood Rail (Aramides wolfi) is a globally threatened, poorly known species endemic to the Chocó rain forests of South America. We provide a first report on the species’ nesting biology, home range, and habitat use. Nests (n = 16) were open cups ~2 m above ground and were more common in secondary forest than expected by chance. Median clutch size was four eggs, incubation lasted >19 days, the precocial young departed the nest within 24 hrs of hatching, and 66% of nests successfully produced young. At least two adults participated in parental care and pair bonds appear to be maintained year-round. The home range of an adult radio-tracked for 7 months was ~10 km2 in selectively-logged forest contiguous to primary forest. This easily overlooked species may be more resilient to moderate levels of habitat degradation than previously suspected, but extensive deforestation throughout its range justifies its current status as ‘Vulnerable to Extinction’. Received 24 February 2010. Accepted 28 July 2010.

Twenty species of Rallidae have become extinct since 1600, and 33 of the remaining 133 extant species (24%) are currently globally threatened (Taylor 1996). Cryptic habits complicate adequate assessment of conservation requirements for many of these species (BirdLife International 2000). For example, population size, conservation status and, in some cases, even geographic distribution of the six species of Wood Rail that comprise the South American genus Aramides are currently unclear (Taylor 1996).

Aramides Wood Rails are relatively large, primarily terrestrial birds that favor more wooded environments than many other rails (Ridgely and Greenfield 2001). Four members of the genus are thought to be globally threatened (Taylor 1996), including the Brown Wood Rail (Aramides wolfi). This species is distributed at lower elevations along the western slope of the Andes in Colombia, Ecuador, and perhaps Peru (BirdLife International 2000). It is recorded from streams and swampy areas inside humid forest and secondary woodlands (Ridgely and Greenfield 2001). The Brown Wood Rail is reclusive, hard to observe, and vocalizes infrequently; its basic biology remains poorly known. Widespread habitat destruction within its range (Sierra 1996, Conservation International 2001) and its apparent absence from many localities (Ridgely and Greenfield 2001), have caused it to be considered ‘Vulnerable to Extinction’ globally (BirdLife International 2000) and ‘Endangered’ in Ecuador (Hilgert 2002). We provide the first detailed report of the basic biology, including nest site selection, nesting biology, and habitat use of the Brown Wood Rail.

METHODS

Field work was conducted at Bilsa Biological Station (79° 45’ W, 0° 22’ N, 330–730 m elevation), a 3,500-ha private reserve operated by Fundación Jatun Sacha within the 70,000-ha Mache-Chindul Ecological Reserve in Esmeraldas Province, Ecuador. Bilsa is approximately two-thirds undisturbed humid rain forest and one-third secondary forests (extensively logged with 10–20 years of regeneration) or selectively-logged forests (high-graded 10–20 years ago). The surrounding area contains patches of primary, selectively logged, and secondary forests interspersed among areas used for cacao (Theobroma cacao) cultivation, grazing livestock, and other agricultural uses.

We conducted systematic surveys for Brown Wood Rail nests throughout Bilsa from January 2007 to January 2009. We monitored activity at nests from blinds using 10× binoculars to record status and behaviors, and recorded nest location and elevation using hand-held global positioning system (GPS) units. We quantified habitat characteristics around all but one nest by measuring canopy height, canopy openness (with a spherical densiometer), and number of trees with diameter at breast height (DBH) between 10 and 50 cm in...
10-m diameter circular plots and >50 cm in 20-m diameter circular plots. We compared these data to equivalent measurements from 87 points at 200-m intervals along 17.5 km of trails in Bilsa that we used to survey for Aramides nests. We classified these 87 points as being in primary, altered, or secondary forest based on visual inspection and knowledge of land use history, and used a discriminant analysis to build a predictive model of group membership based on habitat characteristics. This model correctly assigned 85% of the 87 training points as primary \((n = 41)\), selectively-logged \((n = 23)\) or secondary \((n = 23)\) forest. The two discriminant analysis functions were significant \((\text{Function 1, Wilks' Lambda } = 0.280, P < 0.001; \text{Function 2, Wilks' Lambda } = 0.866, P = 0.008)\) and were subsequently used to classify the type of forest where Brown Wood Rail nests were found.

We captured three adult Brown Wood Rails in mist nets between March 2007 and January 2009, and took morphological measurements and applied three colored leg bands. We applied a lightweight radio transmitter (model PD-2; Holohil Systems, Carp, ON, Canada) using a Rappole harness (Rappole and Tipton 1991) to a breeding individual of unknown gender captured on 12 March 2008. The 3.8-g radio weighed <1% of the bird’s total body mass. We tracked the individual using a TR4 receiver and a RA-2AK ‘‘H’’ antenna (Telonics, Mesa, AZ, USA) until the radio battery failed in November 2008. We suspended radio-tracking during nesting to minimize disturbance. We obtained locations of the bird at 30-min intervals during each radio-tracking session and recorded UTM coordinates using a handheld GPS unit. We plotted these coordinates using the Animal Movement extension in ArcView GIS 3.2 (ESRI 2006) and described home ranges as minimum convex polygons (MCP’s) (Mohr 1947), and 95 and 50% fixed kernel isopleths using least-squares cross validation (Worton 1989, Seaman and Powell 1996). Means ± SD are provided for all measurements.

RESULTS

We found nine active nests and seven additional nests that had evidence of recent activity but which were not active when discovered. Nests were found in February \((n = 3)\), March \((n = 10)\), and April \((n = 3)\). Median clutch size was four eggs \((\text{mean } = 3.7 ± 0.7, \text{range } = 2–4)\). Eggs were oval in shape and cream-colored with brown spotting at the ends; dimensions of one were \(4.7 × 3.5 \text{ cm} (\text{Fig. 1A})\). At least two adults shared incubation duties with replacement triggered by sharp, cracking vocalizations by the arriving adult. At most only a single adult was banded at any given nest, and we could not confirm whether more than two birds incubated. Maximum incubation period observed was 19 days, which should be considered the minimum for this species because all active nests had full clutches with discovered.

Two of nine active Wood Rail nests were apparently depredated, one was abandoned, and six successfully fledged four young each. Hatch ing was synchronous (on the same day) and young left the nest within 24 hrs of hatching. Chicks hatched with eyes open and were brooded almost continuously until departing the nest; we observed no feeding while the chicks were still in the nest. Chick plumage was dark brown with light brown longitudinal streaking and highly cryptic \((\text{Fig. 1B})\), similar to that described for other Rallidae. At least two adults continued to care for the young for up to 10 days of age. Young chicks stayed together and were twice observed among the roots of a palm \((\text{Iriartea deltoidea})\) with stiff roots but were cryptic, moved rapidly, and difficult to observe.

Nests were open cups atop stumps of fallen trees \((n = 5 \text{ cases})\); mean tree DBH = 31.1 ± 16.2 cm, mean tree height = 1.5 ± 0.6 m), at the intersection of multiple trunks and/or lianas \((n = 3 \text{ cases})\); DBH = 5.03 ± 1.0 cm, height = 4.1 ± 2.9 m), or in understory shrubs \((n = 8 \text{ cases})\); DBH = 6.6 ± 3.6 cm, height = 2.8 ± 1.4 m). Average nest height was 1.8 ± 0.5 m \((\text{range } = 1.2–2.6)\) above the ground. Nests were constructed primarily of large, dead leaves \((\text{e.g., Araceae, Cecropiaceae, Piperaceae, and ferns})\) and a few small pieces of dried vine, and were relatively bulky \((\text{exterior dimensions: } 26.8 ± 8.3 \times 28.2 ± 6.0 \times 12.3 ± 4.0 \text{ cm} \text{; interior dimensions: } 12.0 ± 1.7 \times 20.0 ± 2.6 \times 3.8 ± 1.0 \text{ cm})\). The interior was lined with a mixture of live and dead, smaller leaves \((\text{primarily Melastomataceae})\). Nests were constructed beneath leaves and ferns in low light environments, making them relatively cryptic despite their large size \((\text{Fig. 1C})\).

Nests were found in forest areas where elevation averaged 551 ± 31 m asl \((\text{range } = 448–587)\), canopy height averaged 15.2 ± 6.5 m, densiometer measures of canopy openness averaged 14.1 ± 6.9%, and there were 3.13 ± 2.1
trees with DBH between 10 and 50 cm, and 0.44 ± 0.9 trees with DBH > 50 cm. Eleven nests were in secondary forest, four in selectively-logged forest, and one in primary forest. Comparison of nest site to habitat availability in the Bilsa area (based on 87 sampled points) revealed Brown Wood Rails used secondary forests as nesting sites in a larger proportion than this habitat is available in the area we sampled ($\chi^2 = 13.74, P = 0.001$).

Morphological measurements for three individuals of unknown gender were: mass (506.7 ± 61.1 g), tarsus (73.9 ± 1.0 mm), wing chord (175.8 ± 1.8 mm), tail length (52.4 ± 1.7 mm), beak depth (16.5 ± 3.3 mm), beak width (8.9 ± 0.9 mm), culmen from the distal edge of the nare (29.4 ± 1.8 mm), and exposed culmen (55.6 ± 4.1 mm). The eye ring and the iris were intensely bright red in all individuals (Fig. 1D).

We conducted 24 radio-tracking sessions and obtained 150 independent locations of a radio-marked bird of unknown gender between 12 March and 9 October 2008. This individual used a clearly defined territory whose overall MCP home range size was 13.5 ha; 95 and 50% kernel home range sizes were 9.0 and 0.9 ha, respectively. The radio-equipped individual was active throughout the day and at night was observed roosting 5 m above the forest floor in a ~7-m tall Melastomataceae tree, suggesting a diurnal pattern of activity. We opportunistically observed adults eating tadpoles from small puddles (10 cm²) in muddy trails and small streams on five separate occasions.

The radio-marked bird was seen and/or heard with at least one other adult throughout the radio-tracking period. We recorded three distinct types of vocalizations: (1) a sharp, crackling vocalization audible at short distances used when nesting, heard when adults replace each other incubating or when adults called recently-hatched young; (2) a low frequency call audible for long distances used by adults of the same pair, perhaps to establish territoriality; and (3) a loud crackling call also audible over long distances which corresponds to the "kyow" of Ridgely and Greenfield (2001).

**DISCUSSION**

This is the first published account of the nesting biology and home range for any member of the
Aramides Wood Rails, a poorly known neotropical genus with several globally threatened members. Breeding of Brown Wood Rails coincided with peak rainfall and, although the clutch size of four eggs is relatively small compared to other Rallidae (Taylor 1996), nesting success was relatively high (66%). However, post-hatching mortality of young may also be high; at least one adult that successfully hatched young re-nested 14 days later, suggesting the young had been depredated.

At least two adults contributed to incubation, brooding, and post-hatching care. We also observed and/or heard a second individual accompanying a radio-marked bird throughout the 7-month tracking period. We did not observe more than two adults together at any time. These preliminary data suggest Brown Wood Rails may form long-term, socially monogamous pair bonds.

The home range size of 9.0–13.5 ha (95% kernel and MCP, respectively) for Brown Wood Rails is intermediate relative to other terrestrial rain forest species. Home range of the Chestnut Wood Quail (Odontophorus hyperythrus, 275 g) in the Colombian Andes was 5.2 ha (Franco et al. 2006) and home range of the Chowchilla (Orthonyx spaldingii, 150 g) in the Australian Wet Tropics was <2 ha (Jansen 1999). In contrast, the Banded Ground Cuckoo (Neomorphus radiolosus, 433 g) we tracked for a similar time period in Bilsa had a home range of ~50 ha (Karubian and Carrasco 2008). Movements of the radio-marked Brown Wood Rail suggest a clearly demarcated territory, and regular observations of footprints in the established core home range of this individual after the completion of radiotracking suggest year-round residency.

Brown Wood Rails in our study area appeared to exhibit a preference for secondary and selectively-logged forests. The entire home range of the radio-marked individual was restricted to secondary and selectively-logged forest, and a disproportionately high number of nests (15 of 16) we discovered were in secondary or selectively-logged forest. In contrast, the Banded Ground Cuckoo we tracked in the same general area of Bilsa restricted nesting and movements almost exclusively to primary forest (Karubian et al. 2007, Karubian and Carrasco 2008). Some Aramides species have been reported in drier habitats such as deciduous woodlands (Taylor 1996; R. S. Ridgely, pers. comm.), but the Brown Wood Rail may depend upon year-round availability of water; the study area was humid premontane rain forest averaging ~3 m of rain per year (J. Karubian, unpubl. data). All foraging observations were of tadpoles in standing puddles or along creeks, and the individual we tracked was often in close proximity to water or muddy areas.

Brown Wood Rails are cryptic, difficult to observe, unlikely to be captured by passive mist netting, and do not reliably respond to playback making censuses using traditional methods unreliable. Local population size can be estimated with home range data with the caveat these data are only from a lone individual tracked for 7 months. Assuming that Bilsa contains 1,500 ha of suitable habitat (e.g., secondary and selectively-logged forest; Jatun Sacha Foundation, unpubl. data) and that the species forms socially monogamous pairs with territories 10–15 ha in size, Bilsa could possibly support 100–150 pairs. Interviews with local residents and our own observations suggest this species is relatively common when suitable forest occurs outside the boundaries of Bilsa. We observed four old nests (not included in the analyses) and footprints in fragments of secondary forest and cacao plantations outside Bilsa (but <500 m from continuous forest). Our preliminary conclusion is that population size of this species in the 70,000-ha Mache-Chindul Reserve may be several hundred pairs.

Bilsa and surrounding areas where Brown Wood Rail presence was inferred or confirmed consist of a mosaic of habitat types in which secondary forests are often contiguous to primary forest. Brown Wood Rails may persist in and even prefer secondary forests, but more extensive land clearing that increases isolation of forest fragments is likely to adversely affect this species. Our findings suggest Brown Wood Rails may be relatively resilient to intermediate levels of habitat degradation encountered in our study area, but we consider its’ current status as ‘Vulnerable to Extinction’ to be justified given the continued and widespread deforestation occurring throughout its range.

ACKNOWLEDGMENTS

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Committee (ARC 2005-132-01). This project was supported by the Audubon Society (Los Angeles Chapter); Ecociencia; Disney Wildlife Conservation Fund; Chicago Zoological Society; Conservation, Food and Health Foundation; National Geographic Society; and the National Science Foundation (OISE-0402137).

LITERATURE CITED


**ESRI.** 2006. ArcGIS 3.2. Environmental Systems Research Institute, Redlands, California, USA.


Short Communications


First Description of Nests and Eggs of Chestnut-headed Crake
(Anurolimnas castaneiceps) from Ecuador

Galo Buitrón-Jurado,1,2,3 Juan M. Galarza,1 and Danny Guarderas1

ABSTRACT.—We describe the nest and eggs of the Chestnut-headed Crake (Anurolimnas castaneiceps) based on observations of two nests found in the border of the Lliquino River, Pastaza Province, Ecuador. Nests were found in June and December with birds incubating eggs. Both nests were on fallen logs covered by vines and epiphytes in natural small gaps. They were open cups and built principally with dead leaves. The coloration of the eggs was pinkish white with scattered brown spots, similar to other Amazonian rails and crakes. The nests were similar in structure to those of wood rails (Aramides spp.) suggesting a close relationship between Anurolimnas and Aramides. Received 24 May 2010. Accepted 14 October 2010.

Information about nesting of birds such as nest architecture and placement may help clarify either phylogenetic relationships among taxa or selective pressures on breeding biology (Zyskowski and Prum 1999, Greeney et al. 2008). Nesting data are also useful for conservation because they may allow predicting potential impacts of land use practices on bird populations (Monterrubio-Rico and Escalante-Pliego 2006, Greeney et al. 2008).

Crakes, gallinules, and coots (Rallidae) are a nearly cosmopolitan group of marsh- and swamp-inhabiting birds. Some species are common and widespread in many tropical habitats, but information on the natural history of several species remains unknown because of their secretive habits. Details about the breeding biology of eight neotropical species of rails, including the Chestnut-headed Crake (Anurolimnas castaneiceps) are still lacking (Taylor 1996). The range of the Chestnut-headed Crake is in western Amazonia from eastern Colombia to northwestern Bolivia (Hilty and Brown 1986, Tobias and Sheldon 2007). It is a fairly common bird in Ecuador and occurs in secondary woodlands, humid forests, and seasonally-flooded forests in the eastern lowlands (Ridgely and Greenfield 2001). It is a cryptic species and there are few data available about its behavior and natural history. We present the first description of the nest and eggs of the Chestnut-headed Crake from Lliquino River, Pastaza Province in Ecuadorian Amazonia.

METHODS

We conducted several surveys at seven localities as part of a bird diversity study in the Lliquino and Villano river drainages from February to December 2008, Pastaza Province, Ecuador. The Lliquino and Villano rivers are small tributaries of the Pastaza River in the Ecuadorian Amazonia. The area is characterized by continuous lowland evergreen rain forest (Sierra 1999). The forest canopy was 25 m tall with scattered emergent trees 35 m in height. Common tree species included Iriartea deltoidea, Otoba glyciocarpa, Grias neubertii, and several species of Inga. The topography of the basin was hilly and many streams flow through it. The climate is wet and rainy. Climatic data for the locations are not available but the average annual precipitation recorded at the closest meteorological station in Puyo is 4,500 mm (6-year average) (INAMHI 2006).

Nests were discovered inside the vegetation during walks through the area. The first was ~5 km from the Kichwa village of Pandanuque, ~27 km southeast of the town of Sarayacu (01° 44' S, 77° 29' W, 427 m asl), Pastaza Province. The second nest was near the Kichwa village of Huito, ~10 km west of the location of the first nest. Access was by helicopter.

Dimensions of eggs and nests were measured with calipers to the nearest 0.1 mm. The egg found in the second nest was weighed using a pesola scale. Color names follow Smith (1975).
DESCRIPTION OF NESTS AND EGGS

We discovered the first nest at ~1730 hrs on 13 June 2008 with an adult incubating two eggs. It was in a gap within the forest next to a trail, ~200 m from the Lliquino River margin (01° 31’ S, 77° 33’ W, 327 m asl), Pastaza Province, Ecuador. At first contact, the bird’s identity could not be accurately ascertained because it rapidly flushed. However, several photographs were obtained at a later visit in the afternoon of 19 June (Fig. 1A). We found a second nest on 8 December 2008 on the border of the Lliquino River (01° 28’ S, 77° 32’ W, 442 m asl) near the Kichwa community of Huito. An adult flushed quickly from the nest that contained only one egg. We visited the nest during the night of 12 December 2008 to properly identify the nest owner and take photographs (Fig. 2A) and measurements. We visited nests at night because of the tendency of adults incubating both nests to flush when we tried to photograph them during the day.

Birds at both nests were identified as Chestnut-headed Crake because of their chestnut head with an olive-brown mid-line extending from the nape to the back. The bill was black and yellow, legs pinkish red, and irises red (Figs. 1A, 2A).

The first nest (Fig. 1B) was on a fallen tree trunk (69 cm diameter), covered by abundant epiphytes and vines, 1.3 m above ground. Vegetation around the nest was dominated by vines, large-leaved plants (Maranthaceae), Iriarteodeltoidea palms, and Melastomataceae with nearby bamboo (Guadua angustifolia) patches. The canopy above the nest was open, but many live plants around and above the nest provided shade. The nest was oriented to the west and we estimate it received sunlight from mid-day to mid-afternoon. The nest was surrounded by abundant leaves and attached to the twigs of a vine-tangle growing on the trunk. The second nest was also on a fallen trunk, 0.5 m above the ground next to a ravine. The nest was surrounded by abundant vegetation with many vine leaves (Alchornea, Anthurium), which concealed and provided shade to the cup. The second nest was also in a gap with an open canopy.

Both nests were similar in shape. The first nest was a flat and bulky bowl-shaped platform (Fig. 1C). The nest base and exterior consisted of a broad mass of large dead leaves, including an Anthurium (Araceae) leaf with a length of 430 mm. The cup included Virola spp. (Myristicaceae) leaves, as well as woody material (i.e., sticks, vine twigs). Sticks were the main material supporting and surrounded the eggs. Moss abundantly grew over the trunk next to the nest but it was not part of the nest materials. The outer diameter of the nest was 200 × 170 mm (measured at perpendicular angles). The inner cup diameter was 53.9 × 70.1 mm and the depth was 100 mm. The second nest was also a bulky bowl-shaped platform built with many dead
Many dead leaves were the base of the second nest increasing the depth.

Eggs were sub elliptical and pale pinkish buff (Smith 1975: #121D) with a white wash and scattered tiny dark grayish brown (Smith 1975: # 20) marks and spots (Fig. 2C). Dimensions of the egg in the second nest were 38.3 × 28.4 mm and it weighed 16 g.

**DISCUSSION**

The two nests of the Chestnut-headed Crake were similar in building materials and architecture to nests of wood rails (*Aramides* spp.) (Hilty and Brown 1986, Taylor 1996, Vaca et al. 2006; J. Karubian, unpubl. data). These non-aquatic Railidae inhabit tropical lowland rain forest and have nests built with loosely attached leaves. Information concerning nest architecture of *Aramides* is incomplete as nests of two species remain to be described (Taylor 1996). The nest is a bowl-shaped platform for the rest of *Aramides* species and primarily composed of leaves or weeds (Taylor 1996). Nests of the Red-winged Wood Rail (*Aramides calopterus*) and Brown Wood Rail (*A. wolfi*) are bulky bowl-shaped platforms built with twigs and covered by leaves or weeds (Vaca et al. 2006, Carrasco and Mena 2008; J. Karubian, unpubl. data). Species inhabiting more open habitats (scrubby pastures, rice fields), including Giant (*A. ypecaha*) and Gray-necked (*A. cajanea*) wood rails, have nests that are deep bowls which also include green and dead leaves (Taylor 1996, Di Giacomo and Krapovickas 2005). This type of nest is also reported for the Uniform Crake (*Amaurolimnas concolor*), a species closely related to *Aramides* (Stiles 1981).

Nests of the Chestnut-headed Crake, Uniform Crake, and *Aramides* wood rails share a similar bowl shape. They are not domed and are built mainly of leaves and woody material. The nests of the Chestnut-headed Crake differed from those of the Russet-crowned (*Laterallus viridis*) and Black-banded (*L. fasciatus*) crakes. Both species have been included with the Chestnut-headed Crake in *Amaurolimnas* by some authorities (e.g.-Taylor 1996, Remsen et al. 2008) because of their similar plumage pattern. The nest of the Russet-crowned Crake is a ball of dead grass with a side entrance, while that of the Black-banded Crake is a domed and bulky ball of grass with a side entrance (Hilty and Brown 1986, Taylor 1996). This type of nest architecture is similar to that reported for species of *Laterallus* whose nests are
a ball of grasses or a semi-domed cup without leaf masses (Ripley and Beehler 1985, Taylor 1996). Our observations of the nest structure of the Chestnut-headed Crake suggest a closer relationship of this species with *Aramides* and *Anamaloploles* than with the Russet-crowned or Black-banded crakes.

Previous information concerning Chestnut-headed Crakes in the Neotropics reports birds in breeding condition in June (Colombia) and nearly young grown in June (Bolivia) (Hilty and Brown 1986, Taylor 1996). One of our nests coincides with a probable breeding period in June within the end of the wet season in the Ecuadorian Amazon. We observed and photographed a nestling, presumably of a Grey-breasted Crake (*Laterallus exilis*) in a nearby locality in July, suggesting that breeding activity of rallids may occur between May and July in Ecuadorian lowlands, during the rainless period. The breeding season of the Chestnut-headed Crake appears to not be constrained to a short period and it is possible this species is an opportunistic breeder, nesting whenever appropriate conditions exist. This is suggested by the different dates of the two nests we discovered with eggs. Higher breeding activity in northeastern Ecuador has been reported during the months of August to September, although nests have been reported throughout the year for a large variety of avian species (Greeney et al. 2004, Greeney and Gelis 2008). We suggest this topic requires further study because there are few data available concerning breeding season of birds in Ecuadorian Amazonia.

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LITERATURE CITED


Breeding Biology of the Snowy-cheeked Laughingthrush (Garrulax sukatschewi)

Jie Wang,¹,² Chen-Xi Jia,¹ Song-Hua Tang,¹ Yun Fang,¹ and Yue-Hua Sun¹,³

ABSTRACT.—Breeding of the poorly known Snowy-cheeked Laughingthrush (Garrulax sukatschewi) was studied in a conifer-dominated forest at Lianhuashan (southern Gansu), China. Snowy-cheeked Laughingthrushes nested at sites with fewer conifers and denser shrubs compared with the available vegetation. Bowl-shaped nests were 2.4 ± 0.1 m (x ± SE, n = 31) above ground in six plant species. Spruce (Picea spp.) was used (74%) more often than expected based on availability at nest sites. The breeding season (early May to mid Jul) was shorter than for other timaliids. Twelve of 20 (60%) nests with known outcomes were successful. The average clutch size was 3.5 ± 0.2 eggs (2-5, n = 21) with 2.7 ± 0.2 hatchlings (2-4, n = 15) and 2.2 ± 0.2 fledglings (1-3, n = 12) per nest. Incubation was by both males and females and lasted 14 days (n = 1); both parents cared for the nestlings for 16-18 days (n = 3). Received 5 April 2010. Accepted 12 August 2010.

The Snowy-cheeked Laughingthrush (Garrulax sukatschewi) is largely restricted to a range of 28,500 km² in the Min Shan Mountains of southern Gansu and northcentral Sichuan, China at elevations of 2,000-3,500 m (Collar et al. 2001). It is inferred to have a small, declining, severely fragmented population because of the destruction of temperate forests in its range through logging and conversion to agriculture (Collar et al. 2001). The species is categorized as Vulnerable by the IUCN (2009).

Understanding a bird’s habitat requirements, social behavior, and breeding is essential for successful species conservation (Primack 1993). Apart from a few distribution records (Collar et al. 2001) and the description of a few nesting attempts (Li 1993, Bi et al. 2003), there is little published information on the ecology and conservation status of the Snowy-cheeked Laughingthrush. We provide detailed information on the breeding biology of this species with particular emphasis on nest-site selection and breeding parameters.

METHODS

Study Area.—The study was conducted in a conifer-dominated forest in the Lianhuashan Natural Reserve, southern Gansu (34° 57' N, 103° 46' E) as described by Sun et al. (2003). The forest occurs on north-facing slopes at elevations of 2,600–3,300 m; only grasses and shrubs grow on south-facing slopes. Coniferous forest, the most prevalent cover type (42%) in the study area, is dominated by Dragon spruce (Picea asperata) and Fargese fir (Abies fargesii). The other vegetation types are: (1) mixed deciduous-coniferous forest, including variable amounts of willow (Salix spp.) and birch (Betula utilis and B. albo-sinensis), and (2) shrublands, including willow, Sea buckthorn (Hippophae rhamnoides), and barberry (Berberis spp.). Deciduous forest is uncommon in the area and, where it occurs, is adjacent to mixed deciduous-coniferous forest. The mean annual temperature at the study area is ~5.1–6.0°C with a maximum of 34.0°C and minimum of ~27.1°C. The climate is semi-arid, and the annual precipitation is ~65 cm.

Field Procedures.—We located Snowy-cheeked Laughingthrushes during four breeding seasons (Apr–Jul 2003, 2005, 2007, and 2008) and three non-breeding seasons (late Jul–mid Aug and Oct–Dec 2006, Sep 2007–Jan 2008) within 100 m of a 10.3-km long trail system by direct observations, and noted flock size and social interactions. We also played back calls, i.e., “hwii-u, hwii-u” (Collar et al. 2007), of the birds and recorded their response. Nests (27 active and 4 previously used) were located by systematically checking individual trees and shrubs during the breeding seasons.

We measured the following variables for each nest after termination of nesting similar to the method of James and Shugart (1970): altitude, distance to forest edge, species and diameter at

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breast height (DBH) of supporting plants (if ≥2 tree species, all species were recorded), height of the nest above ground, and distance between the nest and the stem of supporting plant. Slope exposure and orientation of the nest relative to the stem of supporting plant were recorded in 45° octants. The surrounding cover was estimated as the average proportion of the nest camouflaged when viewed from three different sides at a distance of 5 m. Overhead cover was estimated as cover that prevented light penetration, in 10% intervals. Locations of nests and inter-nest distances were ascertained with a global positioning system (GPS) (Garmin eTrex Legend® HCx, Olathe, KS, USA).

Habitat structure in a 10 × 10 m plot with each nest site or site where laughingthrushes occurred as the center was also measured. Vegetation type was classified as coniferous forest, mixed coniferous-deciduous forest, deciduous forest, or shrubs. Cover (amount of sky obscured), and the numbers of conifers and shrubs with a DBH of >3 cm were also recorded. We made similar measurements to assess the preference of nesting habitats at 38 available sites within 19 territories (2 sites per territory) for comparison.

We took measurements of the eggs and nestlings, once a nest was located, and monitored the nest every 2–4 days, or 1–2 days at critical times, to ascertain laying date, length of incubation, time to fledging, nestling growth, fledging success, and incidence of nest predation. Laying dates were calculated by backdating for nests located when incubation had already begun or nestlings had hatched, using reproductive parameters obtained from clutches for which complete data were obtained.

Incubation or brooding behavior was documented by occasional observations at four nests from a blind to reduce disturbance. Parental behaviors at one nest (containing 2 nestlings) were recorded during days 9–18 after hatching with an infrared video camera placed 0.5 m above the nest. One bird was caught in a mist net 20 m from the nest and marked with red lacquer spots at the end of the tail to check whether both parents (morphologically indistinguishable) incubate or brood at night. Blood (200 μL) was taken for amplification of the CHD gene using the universal P2/P8 primers to ascertain gender (Griffiths et al. 1998). Data from all years were pooled for analysis using SPSS 13.0 for Windows (SPSS Inc. 2004). The percent values were arcsine transformed for t-tests and all tests were two-tailed. Values are given as mean ± SE.

RESULTS

Habitat Use and Social Behavior.—Singles, pairs, and groups of Snowy-cheeked Laughingthrushes accounted, respectively, for 10, 78, and 12% of observations (n = 132) in the non-breeding season (Sep–Apr). The corresponding figures were 75, 24, and 1% (n = 120) for the breeding season (May–Jun). The mean size of groups was 4.0 ± 0.2 (3–6) in the non-breeding season, and most groups (69%) included four individuals. Snowy-cheeked Laughingthrushes occurred in mixed deciduous-coniferous forests (88%), shrublands (9%), and coniferous forests (3%) at elevations of 2,400–3,200 m during all observations (n = 252). They seldom foraged in the abundant areas of moss and fallen needles under pure conifer stands, and were absent at higher elevations (3,200–3,560 m), dominated by dwarf willows and barberries, and absent at lower elevations (2,100–2,400 m) where crops, low shrubs, and human dwellings predominated.

Snowy-cheeked Laughingthrushes appeared to be territorial in late April and May. Calls of one pair usually resulted in three to five neighboring pairs calling simultaneously (30 occasions). Playback of calls also initiated calling and/or approaches by 1–2 neighboring pairs to the speaker (7 of 20 occasions at 10 territory boundaries). Two pairs were observed chasing each other on the ground and performing a series of rapid pivoting and ducking movements from side to side while calling harshly in mid May (2 occasions), seemingly to defend territories. Distances between the closest nests (found in 2007) averaged 100 ± 30 m (55–250 m, n = 10).

Nest Cycle: Days in Each Period.—Our earliest observation of nest building was on 3 May (2008) and the latest known fledging date was 13 July (2005) with an overall breeding season of ~72 days. Nest building lasted ~8 days (1 nest). There was a full of 9 ± 1 day (7–12, n = 5) after nest completion. Onset of laying extended from 7 May (2008) to 10 June (2005) with a peak in late May. One unspotted greenish-blue egg was laid per day (n = 8 eggs in 2 sufficiently monitored nests). Scattered observations at four nests indicated continuous incubation started after laying of the last egg. All nestlings hatched in the same day (n = 2 nests) after 14 days of incubation (n = 1 nest).
during which each egg lost ~0.07 g (1.2%) of its mass per day on average. Hatchlings, weighing 4.7 ± 0.1 g (4.60-4.75 g; n = 3), were largely naked with dull grayish-red skin and only a few gray-white down feathers on the cap, occipital, middle spinal, and femoral tracts. Nestlings opened their eyes at 7 days of age and fledged at 16–18 days of age (n = 3 nests). Mean nesting mass was 38.9 ± 0.7 g (n = 5) at 15–18 days post-hatching, about 54% of the adult mass (67.8–74.0 g, n = 4). Growth rate (logistic regression model) was estimated to be 0.80 ± 0.01 g/day for three nestlings in one nest.

Nest Location and Description.—Thirty-one nests were in coniferous-deciduous forests (74%) or coniferous forests (26%); they were 13 ± 3 m (2–50 m) from the forest edge, at elevations of 2,500–2,900 m. Laughingthrushes favored northeast-facing slopes (30% of nests) with the mean steepness of 27 ± 1° (5–40°). Nest sites had lower spruce-fir density, higher shrub density, and greater canopy cover and shrub cover than available sites (Table 1), suggesting the birds preferred nest sites with fewer conifers and denser shrubs.

Nests were placed in spruce (74.2%), fir (6.5%), or deciduous shrubs (honeysuckle [Lonicera spp.] 12.9%, willows = 3.2%, vines = 3.2%). Spruce was used more often than expected from observed availability at nest sites (χ² = 144.1, df = 2, P = 0.00). Nests were constructed in three types of positions: 2.0 ± 0.1 m (1.3–2.6 m) out from the trunk in larger conifers (DBH = 34 ± 1 m; n = 13), or touching the trunk (<0.3 m) in smaller conifers (DBH = 9 ± 1 m; n = 11), or attached to the branches and stems of shrubs (DBH = 4 ± 1 m; n = 7). Heights of nests in larger conifers were greater than in smaller conifers and in shrubs (1.9–3.5 vs. 1.5–3.6 vs. 1.1–2.6 m; F₁,30 = 4.2, P = 0.03) with an average of 2.4 ± 0.1 m (n = 31) above ground. The average surrounding and above cover at nests were 57 ± 4% (10–90%, n = 31) and 72 ± 4% (30–100%, n = 31), respectively.

Twenty bowl-shaped nests had a mean inside diameter of 9.7 ± 0.2 cm (8.0–12.3 cm), an outside cup diameter of 16.4 ± 0.5 cm (13.5–22.0 cm), an inside depth of 3.6 ± 0.2 cm (2.0–5.0 cm), and an outside height of 7.8 ± 0.5 cm (5.5–15.5 cm). The inner bowl was lined with leaves of Carex spp. and thin strands from the stems of honeysuckle, raspberry (Rubus pungens), Sorbaria kirilowii, Philadelphus tucanus, and Spiraea spp. The outer bowl was made mostly of twigs, mainly mountain ash (Sorbus spp.), honeysuckle, Rhododendron yarvenfia and Cerasus clarofolia, and a few birches. Nest weight averaged 62 ± 7 g (35–130, n = 13).

Nest Productivity and Success.—The mean clutch size was 3.5 ± 0.2 eggs (n = 21) with 2-, 3-, 4-, and 5-egg clutches accounting, respectively, for 3, 5, 12, and 1 nests. Eggs averaged 27.4 ± 0.2 mm (24.6–30.5 mm) in length and 19.8 ± 0.1 mm (18.4–21.1 mm) in width (n = 54 eggs in 15 nests). The mass of eggs measured prior to incubation was 5.42 ± 0.13 g (4.90–6.05 g, n = 8).

Overall breeding success was 60% for 20 known-fate nests with 2.7 ± 0.2 (2–4) hatchlings (n = 15) and 2.2 ± 0.2 (1–3) fledglings per clutch (n = 12). Six nests failed due to predation (3 each during the incubation and nestling periods). Nestlings in two nests died after a week of rain (15–22 Jun 2007), during which the air temperature averaged only 5.0° C (–0.1–11° C). One to two unhatched eggs disappeared in 5 of 9 nests and 25–50% (1 or 2) nestlings disappeared in 5 of 12 nests during the nestling period. No eggs disappeared in 15 nests during the incubation period.

Parental Duties.—Both males and females participated in building nests, incubating eggs, and provisioning and brooding nestlings. Pairs defended nests by calling vociferously when we checked the eggs or nestlings. Scattered observa-

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**TABLE 1.** Habitat characteristics at nest sites in >14 independent home ranges of Snowy-cheeked Laughingthrushes at Lianhuashan, Gansu, China, during 2003–2008 in comparison with available sites.

<table>
<thead>
<tr>
<th>Habitat components</th>
<th>Nest sites (n = 31)</th>
<th>Available sites (n = 38)</th>
<th>t</th>
<th>p</th>
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<tr>
<td>Canopy cover (%)</td>
<td>Mean 72 SE 4</td>
<td>Mean 55 SE 3</td>
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<td>Spruce-fir density (trees/ha)</td>
<td>455 ± 68</td>
<td>674 ± 66</td>
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<td>Birch density (trees/ha)</td>
<td>206 ± 52</td>
<td>329 ± 59</td>
<td>-1.52</td>
<td>0.13</td>
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<tr>
<td>Shrub density (shrubs/ha)</td>
<td>1,035 ± 95</td>
<td>618 ± 156</td>
<td>-2.17</td>
<td>0.03</td>
</tr>
<tr>
<td>Shrub cover (%)</td>
<td>66 ± 6</td>
<td>32 ± 4</td>
<td>4.27</td>
<td>0.00</td>
</tr>
</tbody>
</table>
tions indicated both parents took turns incubating during the day, achieving constant coverage other than one absence of only 24 sec. Six on-nest bouts were 60, 71, >45, >50, <112, and <125 min, respectively. Only the marked bird (i.e., female) incubated at night (4 observations).

Video recordings at one nest (86.8 total hrs) indicated both adults brooded the young in the day but not at night on days 9–18 of the nestling period. Diurnal activities ended at 1841 hrs ± 10 min in 6 days. Length of on-nest bouts decreased slightly as nestlings grew larger, whereas length of off-nest bouts increased with means of 12.3 ± 0.9 min (2–65 min) and 18.8 ± 1.8 min (1–133 min), respectively. Brooding attentiveness decreased from 57% (day 11) to 21% (day 17), except for a sharp rise (58%) on day 14. Parents provisioned nestlings at a frequency increasing from 2.0 (day 11) to 6.0 times/hr (day 16) and decreased to 0 times/hr (day 18) with an overall average of 4.0 ± 0.2 times/hr (0–9 times/hr). Adults provisioned nestlings more intensively in the morning than in the afternoon, but with two peaks at 1200–1300 and 1700–1800 hrs. Frequency of removing (or eating) feces from the nest averaged 1.5 ± 0.2 times/hr (0–4 times/hr, n = 65). The two young fledged synchronously at 0713 hrs on day 18.

**DISCUSSION**

**Nesting Phenology and Nests.**—Egg-laying (7 May–10 Jun) by Snowy-cheeked Laughingthrushes was similar to the Giant Babax (Babax waddelli) (Lu 2004). It was shorter than other common Garrulax species at similar latitudes, including Plain Laughingthrush (G. davidi) (late Apr–late Jul; Luo et al. 1992) and Brown-cheeked Laughingthrush (G. henrici) (May–Aug; Lu et al. 2008).

Nests of Snowy-cheeked Laughingthrush were placed higher than those of other Garrulax species in low bushes (1.1–3.8 vs. 0.5–1.5 m) (Cheng et al. 1987, Ali and Ripley 1996, Lu et al. 2008). Nest sites were lower than those of Giant Laughingthrush (G. maxima) (2.4–7.0 m), which were built in conifers (Wang et al. 2010).

**Nesting Success.**—We observed partial loss of broods and unhatched eggs, possibly removed by parents but not predators. Similarly, the Chinese Hwamei (G. conorus) was reported to move eggs to a new nest when adults found people approaching the ongoing nest (Zhang 2002). Human predation of eggs or nestlings was not considered a threat, as local people were discouraged from frequenting our study area because of research on other endemic birds. Possible predators range from the diurnal Spotted Nutcracker (Nucifraga caryocatactes), Northern Goshawk (Accipiter gentilis), and Siberian chipmunk (Eutamias sibiricus) to the nocturnal leopard cat (Prionailurus bengalensis), all of which are common in the study area.

**Social Unit and Breeding Density.**—Snowy-cheeked Laughingthrushes were in pairs (78%) during the non-breeding seasons, and most groups (69%) appeared to be units of two pairs, as two birds each foraged close and moved in different directions when we approached, similar to the previous description “It was in pairs in both winter and summer” (Dresser and Morgan 1899:271).

The Snowy-cheeked Laughingthrush has been described as “rare”, “fairly common”, and “uncommon” (Collar et al. 2001). The shortest distance (55 m) between nests was greater than that of Elliot’s Laughingthrush (G. elliottii) (30 m, Li and Huang 1991; 35 m, Jiang et al. 2007). Ten active nests were found in an area of 1.2 km² in 2007 (17 birds/100 ha), suggesting the density of Snowy-cheeked Laughingthrush is possibly moderate in the well-managed natural reserve.

**CONSERVATION IMPLICATIONS**

Spruce rather than fir was highly selected as nest substrates (70 vs. 6%), even though both are dominant (513 ± 71 vs. 161 ± 42 trees/ha, Sun et al. 2007), possibly because firs mainly occur inside coniferous forest, where the birds seldom nest. Snowy-cheeked Laughingthrushes preferred to nest in spruce and forage in mixed deciduous-coniferous forest, indicating the presence of spruce with abundant shrubs may be essential habitat requirements and the importance of protecting alpine scrub vegetation adjacent to and within the coniferous forest.

The birds at Lianhuashan were restricted to narrower altitudes (2,400–3,200 m) than has been reported by others (2,000–3,500 m; Stattersfield et al. 1998), possibly due to previous logging and conversion of forest to croplands. The forest in the Lianhuashan Mountains is highly fragmented and 77% of forest patches are smaller than 10 ha due to logging over the past 30–40 years (Sun et al. 2006). Arrow bamboo (Sinarundinaria nitida) clumps within the coniferous and coniferous-deciduous forests were nearly clear-cut by local people. The short breeding season, the degraded
and fragmented habitat, and the restricted range suggest the critical vulnerability of the Snowy-cheeked Laughingthrush.

ACKNOWLEDGMENTS

We are grateful to staff members of our research group and the Lianhuashan Natural Reserve, including Y.-X. Jiang, J.-L. Li, Y.-S. Zhang, X.-S. Liu, P.-P. Luo, and H.-Z. Chang for field assistance. We sincerely thank two anonymous reviewers, C. E. Braun, Gang Song, and J.-Z. Chen for comments on the manuscript, and Dan Strickland for help with English. Financial support was provided by the Chinese Academy of Sciences (Grant kscx2-yw-z-1021) and the National Natural Science Foundation of China (Grant 30620130110).

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Reproductive Status of the Shiny Cowbird in North America

William Post1,3 and Paul W. Sykes Jr.2

ABSTRACT.—We collected 17 (13 females, 4 males) Shiny Cowbirds (Molothrus bonariensis) during the passerine nesting season in July 1999 and 2003 in Jasper County, southwestern South Carolina. Five females (38%) were laying eggs, as ascertained from the condition of their reproductive organs. Two females collected on 1 July 1999 and 19 July 2003 had eggs in their oviducts, and would have deposited eggs within 1 day. Shiny Cowbirds have been in North America for at least 24 years, but only males had been collected before this study. Most of those collected had enlarged testes, as did the four collected in the present study, but these data are not proof that breeding actually occurred. The reproductive condition of the females we collected provides material evidence that the species breeds in North America. It is not known which species are being parasitized by Shiny Cowbirds, but several species widespread in the southeastern United States are highly suitable hosts. Received 23 August 2010. Accepted 3 November 2010.

METHODS

The study area bordered a dredge spoil-site next to the Savannah River in southwestern Jasper County, South Carolina (32° 04′52″ N, 80° 57′83″ W). We captured Shiny Cowbirds in mist nets placed in coastal scrub at the edge of the spoil-site. About 30% of the net site consisted of open ground, either bare or covered with patches of grasses and forbs <30 cm in height. The remainder consisted of stands of woody vegetation which, in order of importance, were composed of hackberry (Celtis laevigata), cherry (Prunus spp.), sweet gum (Liquidambar styraciflua), and blackberry (Rubus spp.).

We captured birds at one site, using three mist nets (6 m length, 30 mm mesh) placed in a triangular array around an elevated feeder provisioned with millet (Panicum milleaceum) seeds (Sykes 2006). The cowbirds were euthanized and then frozen. We recorded diameters of the three largest follicles and of any oviducal egg, the area (length X width) of the ovaries (females), and the dimensions of the testes (males) during examination of the thawed specimens. We assigned age of the birds from plumage characteristics (Pyle 1997). Female Shiny Cowbirds and Brown-headed Cowbirds are about the same size, based on birds collected in or near our study site (mean mass of 13 M. ater = 34.2 g; 13 M. bonariensis = 33.6 g). We assumed the reproductive physiology of the two species is similar, and used the criteria of Scott and Ankey (1983) to ascertain laying rates. We estimated that laying would occur (1) within 1 day if an egg was in the oviduct, or (2) within 2 days, if the ovaries contained at least one laided eggs. breeding can be verified by finding Shiny Cowbird eggs or young associated with an identified host species, and by genetic analysis of eggs, nestlings, and fledglings to distinguish them from Brown-headed Cowbirds.

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pre-ovulatory (round, cream-colored or yellowish) follicle >7.9 mm diameter. Specimens were identified by bill shape and wing formula (Pyle 1997) and were saved as study skins. Identities were verified by comparisons with a series of M. b. minimus collected in the West Indies.

RESULTS

We collected 17 (13 female and 4 male) Shiny Cowbirds in 1999 and 2003. We collected nine females on 1–2 July 1999; six were after-second-year (ASY) and three were second-year (SY) birds (Table 1). One ASY female (Charleston Museum # 05.2.036), had an oviposited (oviducal) egg 13 mm in diameter, indicating she would have laid an egg within 1 day. Another ASY female (# 99.22.037) with an unovulated follicle 8.8 mm diameter, had an extremely dilated cloaca, and presumably had laid an egg the day she was captured. Two SY females (# 99.22.048 and # 99.22.069) had follicles >7.9 mm diameter, and would have laid eggs within 2 days.

We captured four females (3 ASY and 1 SY) on 18–19 July 2003; one ASY female (# 05.2.033) had an oviposited egg 10.3 mm in diameter, and we estimate she would have laid within 1 day; the other three were not laying (Table 1). Thus, five (38%) of the 13 females we examined were judged to be laying.

Four males collected on 1–2 July 1999 had enlarged testes. The lengths of the largest testes of two ASY males were 8.4 and 7.3 mm; those of two SY males were 6.2 and 6.3 mm. The testes of non-breeding Shiny Cowbirds usually diminish to <2 mm in diameter (WP, unpubl. data). Neither males nor females were molting.

DISCUSSION

The first suggestion that Shiny Cowbirds breed in North America was based on a 1991 observation near Homestead, Florida. A Red-winged Blackbird (Agelaius phoeniceus) was seen feeding a "very young" Shiny Cowbird which was "just starting song" (Pranty 2000: 516). The report is questionable, because fledglings of the Brown-headed Cowbird and Shiny Cowbird are not known to sing (Lowther 1993, Lowther and Post 1999) and, if they do, it is not known if their vocalizations can be used to differentiate them. Larry Manfredi (pers. comm. in Pranty 2000) saw a female cowbird, which he identified as a Shiny Cowbird, in April 1998, near Kendall, Florida, fly to an unattended Red-winged Blackbird nest. The cowbird sat on the nest 3–4 min, but it is not known if she laid an egg (Pranty 2000).

Enlarged testes suggest the possibility of breeding, but verification depends on the reproductive status of females. The four males collected in this study had enlarged testes, as did one collected 10 August 2000 at the same site. Seven males collected in South Carolina and Florida during 30 April–25 July 1989–1991 had enlarged testes (Post et al. 1993). A male obtained at Ft. Hood, Texas on 23 May 1990 had enlarged testes (Greg Lasley, pers. comm.) as did one collected 21 May 2009 on Sullivan's Island, South Carolina (WP, unpubl. data).

We provide evidence that Shiny Cowbirds were laying eggs in South Carolina in 1999 and, based on the sizes of preovulatory follicles and the presence of oviducal eggs, estimate that five (38%) of 13 females collected in South Carolina in 1999–2003 were laying (Table 1). Additional evidence of breeding in North America has been provided by collection of two females, each with an egg in her oviduct: in Georgia in 2000 (Sykes and Post 2001), and in northcentral Florida in 2009 (Reetz et al. 2010).

Shiny Cowbirds occur during the passerine breeding period on the Atlantic and Gulf coasts from South Carolina to Alabama (Lowther and Post 1999, Pranty 2000). They have been in the southeastern U.S. at least 24 years; this study and those of Sykes and Post (2001) and Reetz et al.

<table>
<thead>
<tr>
<th>Charleston Museum specimens #</th>
<th>Date</th>
<th>Age</th>
<th>Area of ovaries (mm²)</th>
<th>Diameter (mm) of:</th>
</tr>
</thead>
<tbody>
<tr>
<td>99.22.075</td>
<td>1 Jul 1999</td>
<td>SY</td>
<td>2.3</td>
<td>Largest follicle</td>
</tr>
<tr>
<td>02.46.051</td>
<td>1 Jul 1999</td>
<td>ASY</td>
<td>71.4</td>
<td>Oviducal egg</td>
</tr>
<tr>
<td>05.2.036</td>
<td>1 Jul 1999</td>
<td>ASY</td>
<td>117.5</td>
<td></td>
</tr>
<tr>
<td>05.2.043</td>
<td>1 Jul 1999</td>
<td>ASY</td>
<td>110.0</td>
<td></td>
</tr>
<tr>
<td>05.2.044</td>
<td>1 Jul 1999</td>
<td>ASY</td>
<td>41.9</td>
<td></td>
</tr>
<tr>
<td>99.22.037</td>
<td>2 Jul 1999</td>
<td>ASY</td>
<td>160.2</td>
<td></td>
</tr>
<tr>
<td>99.22.048</td>
<td>2 Jul 1999</td>
<td>SY</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>99.22.069</td>
<td>2 Jul 1999</td>
<td>SY</td>
<td>116.5</td>
<td></td>
</tr>
<tr>
<td>99.22.072</td>
<td>2 Jul 1999</td>
<td>ASY</td>
<td>13.3</td>
<td></td>
</tr>
<tr>
<td>05.2.041</td>
<td>18 Jul 2003</td>
<td>SY</td>
<td>32.0</td>
<td></td>
</tr>
<tr>
<td>05.2.033</td>
<td>19 Jul 2003</td>
<td>ASY</td>
<td>21.8</td>
<td></td>
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<tr>
<td>05.2.040</td>
<td>19 Jul 2003</td>
<td>ASY</td>
<td>33.0</td>
<td></td>
</tr>
<tr>
<td>05.2.042</td>
<td>19 Jul 2003</td>
<td>ASY</td>
<td>30.0</td>
<td></td>
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</table>
(2010) confirm that females are breeding, but it is not known which species they parasitize. Several hypotheses may explain why no information is available. (1) Competition with Brown-headed Cowbirds. This hypothesis is difficult to test, because of the scarcity of both species of cowbirds in regions where they co-occur (Post and Gauthreaux 1989, Stevenson and Anderson 1994, Beaton et al. 2003). Parasitism rates are low: Whitehead et al. (2002) on the central coast of South Carolina found only 13% of 346 nests parasitized, all by Brown-headed Cowbirds. Prather and Cruz (2002) in southwestern Florida found only 2% of 108 nests parasitized. Other studies in the southeastern U.S. have found cowbird-parasitized nests (Sargent et al. 1997, Kilgo and Moorman 2003) but, on the upper coastal plain and piedmont, outside the range of the Shiny Cowbird. (2) The similarity of eggs and young of the two cowbird species. This hypothesis has not been tested, because studies conducted in areas where Shiny Cowbirds occur have documented few cases of parasitism by any cowbirds (Prather and Cruz 2002); another study found cowbird eggs, but all were believed to have been laid by two color-banded Brown-headed Cowbirds (Whitehead et al. 2000). (3) Lack of research in areas occupied by Shiny Cowbirds. This cowbird occurs on the coast from Alabama to South Carolina during the passerine breeding period but, other than Prather and Cruz (2002) and Whitehead et al. (2002), no recent studies of breeding songbird communities on the coast appear to have been published.

Several species widespread in the southeastern U.S. are parasitized by Brown-headed Cowbirds and presumably would be used by Shiny Cowbirds, Whitehead et al. (2002) found 37% of 30 Yellow-breasted Chat (Icteria virens), 36% of 14 Painted Bunting (Passerina ciris), and 24% of 17 Blue Grosbeak (P. caerulea) nests parasitized in coastal South Carolina. The clutch sizes of three species were reduced by cowbird parasitism, and the seasonal fecundity of Blue Grosbeaks was lowered (Whitehead et al. 2000). These authors found two Red-winged Blackbird nests parasitized. This species is potentially a highly suitable host, considering its similarity to the Yellow-shouldered Blackbird (Agelaius xanthomus), which is heavily parasitized in Puerto Rico (Post 1981). Prather and Cruz (2002) also found Red-winged Blackbirds parasitized in southern Florida, where they nests in mangroves, the habitat in which Shiny Cowbirds most often breed in Puerto Rico (Post and Wiley 1977), and in cordgrass (Spartina alterniflora), which is similar to graminoid vegetation used by Yellow-hooded Blackbirds (Chrysomus icterocephalus) parasitized by Shiny Cowbirds in Trinidad (Cruz et al. 1990).

The Shiny Cowbird's population growth is correlated with a decrease of Yellow-shouldered Blackbirds in Puerto Rico (Post 1981), but cowbird control appears to have helped in slowing the blackbird's decline (Wiley et al. 1991, Cruz et al. 2005). If Shiny Cowbirds continue to increase in North America, it is important to examine their effect on potential hosts such as Painted Buntings, which, because of other factors, are already at risk in portions of their range (Sykes and Holzman 2005, Sykes et al. 2006).

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The paper benefited from the reviews and useful comments of Peter Lowther, an anonymous reviewer, and the editor of this journal. Steve Calver, U.S. Army Corps of Engineers, arranged access to the study site.

LITERATURE CITED


Shift to Later Timing by Autumnal Migrating Sharp-shinned Hawks

Robert N. Rosenfield, Dan Lamers, David L. Evans, Molly Evans, and Jenna A. Cava

ABSTRACT.—Increasing proportions of Sharp-shinned Hawks (Accipiter striatus) migrated later in autumn at the Hawk Ridge Bird Observatory, Duluth, Minnesota during 1974-2009. Migration averaged about 4 days later over 35 years since 1974, and about 8 days later during late September through October in the last 16 years of the study. Our results augment previous findings demonstrating recent shifts in phenological events for birds. The proximate causes and potential consequences of this later timing of migration should be investigated. Received 22 March 2010. Accepted 27 July 2010.

Earlier timing of spring migration and egg-laying have been documented in relation to higher spring temperatures in a wide variety of temperate-zone birds in the Northern Hemisphere (e.g., Jenni and Kery 2003, Lyon et al. 2008, Miller-Rushing et al. 2008). Changes in bird migration times, with most attention on spring migration of passerines, are among the best-documented biological responses to increased temperatures (Miller-Rushing et al. 2008).

Our objective was to investigate timing of autumnal migration of Sharp-shinned Hawks (Accipiter striatus) at Hawk Ridge Bird Observatory during 1974-2009. We chose the Sharp-
shinned Hawk as a focal species because its migration is likely linked to spatial and temporal movement of its neotropical songbird prey (Rosenfield and Evans 1980, Viverette et al. 1996, Goodrich and Smith 2008).

METHODS

Study Site and Data Collection.—The Hawk Ridge Bird Observatory (HRBO) is in boreal forest at the western end of Lake Superior in Duluth, Minnesota (49° N, 92° W), and is a well known concentration point for migrant raptors (Goodrich and Smith 2008). Raptors are counted hourly at HRBO from about 15 August through 30 November using standardized techniques established by the Hawk Migration Association of North America (HMANA) (Ruelas Inzunza 2005, Farmer et al. 2008). Detailed descriptions of daily and seasonal coverage of counts at HRBO are provided by Farmer et al. (2008). Migration of Sharp-shinned Hawks primarily occurs from mid-August through October at HRBO with peak monthly totals of migrating birds typically occurring in September (Rosenfield and Evans 1980, Goodrich and Smith 2008). We obtained HRBO count data for Sharp-shinned Hawks during 1974-2009 from HMANA’s Hawkcount.org/month web site (www.hawkcount.org/month_summary.php).

Data Analyses.—We used simple linear regression to assess how Julian date for the 50th percentile of the total number of autumnal migrating hawks in each of 36 study years changed across time (i.e., to ascertain if a shift in migration had occurred). We also used Julian dates for four percentiles (25, 50, 75, and 99.5) of total migration counts in each year to describe the extent of the shift (in days) of the migration. We truncated the 100th percentile at 99.5 to minimize the effect of late-migrating “stragglers” that might skew results. We calculated the difference in number of Julian dates (days) for each percentile in each year for 1975-2009 relative to Julian dates for the respective percentiles in 1974, the first year of the study. Julian dates earlier and later than those in respective percentiles for 1974 were assigned negative and positive values, respectively. We used the average (± SE) of those differences to enumerate the approximate shift in days in migration for each respective percentile since 1974. We chose 1974 as the comparative year to demonstrate the extent of the shift in timing of migration because it was representative of the earlier timing of migration at the outset of the study (Fig. 1). We also report the shift for all combined percentiles, 1975-2009. Further, we separate the percentiles in the first 19 years of study (1975-1993) from those during...
TABLE 1. Timing of autumnal migration of Sharp-shinned Hawks at Hawk Ridge Bird Observatory, Duluth, Minnesota, 1974–2009. Julian dates for 1974 indicate when the specified proportion of the total number of migrating hawks was attained; Julian dates for other years are rounded approximations of percentile attainment based on mean values (in parentheses ± SE) of shift in days relative to Julian dates in 1974. Calendar dates are provided for descriptive reference.

<table>
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<tbody>
<tr>
<td>25</td>
<td>254; 11 Sep</td>
<td>253 (−1.37 ± 0.85)</td>
<td>257 (2.5 ± 0.96)</td>
<td>254 (0.4 ± 0.71)</td>
</tr>
<tr>
<td>50</td>
<td>258; 15 Sep</td>
<td>261 (3.16 ± 0.77)</td>
<td>266 (7.69 ± 1.0)</td>
<td>263 (5.23 ± 0.72)</td>
</tr>
<tr>
<td>75</td>
<td>269; 26 Sep</td>
<td>272 (2.63 ± 0.75)</td>
<td>278 (8.87 ± 0.83)</td>
<td>275 (5.49 ± 0.76)</td>
</tr>
<tr>
<td>99.5</td>
<td>289; 16 Oct</td>
<td>293 (3.47 ± 0.87)</td>
<td>298 (9.3 ± 0.99)</td>
<td>295 (6.14 ± 0.82)</td>
</tr>
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</table>

the last 16 years (1994–2009) because a greater shift occurred since 1994. We calculated probability values using SYSTAT (Wilkinson 1992). Statistical significance was accepted at α ≤ 0.05.

RESULTS

There was a statistically significant increase in Julian dates for the 50th percentile of the seasonal totals of migrating Sharp-shinned Hawks across 36 years at HRBO (Fig. 1); greater proportions of hawks were migrating later in autumn. The extent of the shift was on average ~3 days later in the second through fourth percentiles during the first 19 years since 1974 (1975–1993), but increased to a consistent average of ~8 or 9 days later compared to 1974 in the second through fourth percentiles during 1994–2009 (Table 1). Twenty-two (29%) of the 76 total Julian dates registered an earlier day of percentile attainment during 1975–1993 versus 1974 (9 of the 22 earlier dates occurred in percentiles >25%). Only 5% (n = 3) of 64 Julian dates were earlier during 1994–2009 versus 1974 (all earlier dates occurred in the first percentile; i.e., the first month of migration). There was a consistent later shift in the last 1.5 months of migration during the last 16 years of the study. The shift in migration was on average 4.31 (±0.42) days later for all percentiles combined, and consistently ~5 days later on average in the last three percentiles across 35 years since 1974 (Table 1).

DISCUSSION

This study is to our knowledge the first to show a shift in timing of the autumnal migration of a raptor. We demonstrated that Sharp-shinned Hawks since 1974 have migrated on average ~4 days later at HRBO during 1975–2009. We speculate on possible factors influencing this phenomenon.

There is a sequence in movements of age cohorts of Sharp-shinned Hawks at HRBO: juvenile birds (<1 yr) precede adults (≥2 yrs) by ~2 weeks and, within age groups, females precede males by ~1 week (Rosenfield and Evans 1980). This sequence in the migration of cohorts, as indexed by trapping data obtained during the same days and months in each year that counts are conducted at HRBO, has not changed during our study years (DLE and RNR, unpubl. data). It appears that juveniles still migrate principally during the first month of migration, and adults predominate in the last 1.5 months (DLE and RNR, unpubl. data). Precisely which cohort movements may have changed temporally in the overall migration of Sharp-shinned Hawks at HRBO is not known because counters cannot identify age and gender of the majority of migrating individuals.

About 13,300 Sharp-shinned Hawks were counted at HRBO annually during 1974–2009. Farmer et al. (2008) reported a low, non-significant, average percent change per year (~0.7) for Sharp-shinned Hawks observed at HRBO across most of our study years (1974–2004) based on standardized count effort. Sharp-shinned Hawks moving through HRBO originate from northern Minnesota and a large part of interior and, possibly, western Canada (Evans and Rosenfield 1985, Goodrich and Smith 2008). The long-term duration of our study ensures that we have cross-generational data for Sharp-shinned Hawks (Bildstein and Meyer 2000). The long-term shift in timing of the migration we documented is not likely due to variation in inter-year counts of migrating birds (cf. Miller-Rushing et al. 2008), or to behavioral plasticity of an age cohort (cf. Miller-Rushing et al. 2008), nor to some local geographical effect (Lyon et al. 2008).

Climate change may have an influence on the availability of food for higher trophic species such as birds as a result of advanced phenology of lower trophic organisms and a prolonged summer season (Penuelas and Filella 2001). Several
European passerines have delayed autumn migration, although other species have advanced departure dates (Jenni and Kery 2003). It is possible the migratory songbird prey of Sharp-shinned Hawks in boreal forests north of HRBO (Bildstein and Meyer 2000) could delay their migration if their food was available for longer summers (cf. Penuelas and Filella 2001), which in turn could cause a later migration of hawks that track the movement of passerines. Raptorial species, such as accipiters, use powered flight for migration and must hunt regularly while on migration (Ydenberg et al. 2007, Goodrich and Smith 2008). However, we know of no data indicating temporal changes in autumnal songbird migrations north of or at HRBO (G. J. Neimi, pers. comm.).

A possible explanation for the shift in timing may be migratory short-stopping, whereby Sharp-shinned Hawks north of HRBO may be moving less, and perhaps less per day, in response to increased prey availability (possibly at bird feeders) north of HRBO. This could result in hawks taking longer to pass through HRBO. This phenomenon was suggested as one explanation for declining, inter-year autumnal numbers of Sharp-shinned Hawks observed at Hawk Mountain, Pennsylvania and Cape May Point, New Jersey (Viverette et al. 1996). However, there has been no significant inter-year variation in counts of Sharp-shinned Hawks at HRBO. Further, the decline in observations of Sharp-shinned Hawks at Cape May particularly involved juveniles (Viverette et al. 1996), and the shift in later timing of migration at HRBO is likely by adults.

There is no pattern of agreement in trends of counts of migrating Sharp-shinned Hawks at different watch sites (including HRBO) in eastern North America. This suggests there is considerable spatial structure in a regional population or that migration geography varies with sub-region (Farmer et al. 2008).

Our results augment findings demonstrating recent shifts in phenological events for birds and other animals (Root et al. 2003, Crick 2004, Miller-Rushing et al. 2008), and we examined factors possibly altering the timing of Sharp-shinned Hawk autumnal migration in northcentral North America. The potential proximate causes, such as the timing of autumnal songbird migration north of HRBO, and the consequences of the later timing of migration of hawks should be investigated. Changes in environmental conditions could influence the survivorship of maladjusted individuals given potential decoupling between migration schedules of Sharp-shinned Hawks and their songbird prey (Both et al. 2006, Heller and Zavaleta 2008).

ACKNOWLEDGMENTS

We thank the many individuals who counted migrating birds of prey at HRBO. Partial funding for this study came from the Personnel Development Committee at the University of Wisconsin at Stevens Point. This manuscript was improved by the comments of E. A. Anderson, John Bielefeldt, T. L. Booms, M. A. Bozek, C. E. Braun, W. E. Stout, and two anonymous reviewers.

LITERATURE CITED


Lunar Influence on the Fall Migration of Northern Saw-whet Owls

Jackie Speicher,1,2 Lisa Schreffler,1 and Darryl Speicher1

ABSTRACT.—Seasonal migration is an important component in the life cycle of Northern Saw-whet Owls (Aegolius acadicus). We evaluated the influence of the four lunar events (new moon, first quarter moon, full moon, and last quarter moon) on nocturnal activity of Northern Saw-whet Owls based on captures during fall migration, 2000–2008. We found differences between the lunar events with decreased capture rates during the full moon and the new moon. These results suggest lunar phase influences migratory movements and behaviors in this species. This may be attributed to predator avoidance during periods of relative brightness or darkness at night. Received 10 July 2009. Accepted 19 October 2010.

The amount of light at night should be an important variable to nocturnal migrants. One potentially important influence on timing of flights is the lunar cycle, which is described by its four predictable conditions (first quarter moon, full moon, last quarter moon, and new moon). Pyle et al. (1993) reported that decreased lunar light was correlated with an increased number of departures during fall migration by landbirds. Moonlight affects behavior by either increasing foraging behavior or predator avoidance. Leach’s Storm Petrels (Oceanodroma leucorhoa) decrease activity during times of increased moonlight when
gull (Larus spp.) predation rates are relatively high (Watanuki 1986). This behavior modification suggests that petrels assess the risk of predation. Tropical Nightjars and other caprimulgids also increase foraging activity during periods of lunar illumination (Brigham and Barclay 1992, Jetz et al. 2003). Changes in feeding behavior in association with changes in moonlight have also been noted for small mammals which are prey species (Price et al. 1984, Gannon and Willig 1997, Lang et al. 2006, Schmidt 2006). Foraging activity typically decreases with increased lunar light.

The Northern Saw-whet Owl (Aegolius acadicus) is a short-distance migrant that breeds in coniferous or mixed deciduous forests of North America. The adults are approximately 15–21 cm long (wingspan: 43 cm). Their weight ranges from 65 to 151 g with females averaging slightly larger than males (Cornell Laboratory of Ornithology 2009). Northern Saw-whet Owls prey primarily on small rodents, including mice (Peromyscus spp.) and voles (Microtus spp.).

The Northern Saw-whet Owl is also the potential prey of larger owls. Competing biological needs likely mean that owls react to lunar events in the context of foraging, avoiding predation, and movement. The full moon would be predicted to increase vigilance for predators leading to a decrease in foraging effort. Light conditions may also prompt a temporary pause in migratory flights or extended stopovers. We assessed the influence of the lunar condition on the capture rate of Northern Saw-whet Owls.
SHORT COMMUNICATIONS

FIG. 1. Mean (± SE) capture rates (birds/net hr) of Northern Saw-whet Owls during the four lunar events (n = 178 individuals).

Saw-whet Owls to examine if illumination was a factor in timing of migration.

METHODS

The study area was in Skytop, Pennsylvania (41° 22' N, 75° 24' W, elevation 513 m) on the south side of West Mountain. It is a semi-permanently flooded cold deciduous forest dominated by eastern hemlock (Tsuga canadensis), red maple (Acer rubrum), and rhododendron (Rhododendron carolinensis). Northern Saw-whet Owls were not recorded at this location before this study and their status as residents remains unknown.

The study period lasted from 1 October to 15 November, 2000-2008. Each calendar day was assigned a corresponding lunar cycle code from one to 28 (NASA 2009). Day 1 represents the new moon, day 7 represents the first quarter moon, day 14 represents the full moon, and day 21 represents the last quarter moon.

Five mist nets (12 × 2.5 m × 60 mm mesh) were placed in a continuous line oriented in a north-south direction. A conspecific audio lure was positioned at the center of the net array. Nets were opened each evening from 1900 to 2300 hrs and mist nets were visited every 30 min. Individuals captured were weighed (g), measured, banded, and released using standard Bird Banding Laboratory protocols. Data were recorded for each encountered individual.

We calculated the rate at which owls were captured each evening by dividing the total number of birds caught by each evening’s net effort. Data were pooled and averaged for each lunar day. Data were analyzed using ANOVA.

RESULTS

Each field season included all four lunar events (first quarter moon, full moon, last quarter moon, and new moon). No significant difference in net hours was evident between the four individual lunar events. No significant differences in capture rate were evident between each of the four lunar events (ANOVA: df = 3, P = 0.09) (Fig. 1). Mean capture rate was lowest during the new moon and full moon. The only exception to this pattern occurred in 2004 when there was an increase in captures associated with a total lunar eclipse.

DISCUSSION

Weather variables including precipitation, high winds, and cloud cover had a negligible effect on capture data during the 9-year study. However, there was a decrease in capture rates during the full and new moon relative to the last quarter moon.
ACKNOWLEDGMENTS

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LITERATURE CITED


CORNELL LABORATORY OF ORNITHOLOGY. 2009. All about birds: Northern Saw-whet Owl, Laboratory of Ornithology, Cornell University, Ithaca, New York, USA. http://www.allaboutbirds.com


ABSTRACT.—Nocturnal migration is a common strategy among North American passerines. Birds of the Fringillidae have typically been labeled as predominately diurnal migrants. We used pressure-zone microphones and automated sound detection software to record flight calls of nocturnally migrating birds from 2 to 16 October 2008 from 2000 to 0600 hrs EST at three locations near Gardiner, Maine. We detected and recorded 190 Pine Siskins (Spinus pinus) flight calls from throughout the night at three separate locations. This is the first published documentation of apparent nocturnal migration in this species. Nocturnal migration may be a facultative migration strategy in the Fringillidae that occurs only in years in which large irruptive movements occur as for Pine Siskins in fall 2008.

Received 30 October 2009. Accepted 3 November 2010.

Most North American passerines are known to be nocturnal migrants. Theories for why nocturnal migration is more common than diurnal migration among passerines include: nocturnal migration maximizes day-time feeding opportunities, provides more stable atmospheric conditions for migration, allows migrating birds to take advantage of cooler temperatures to lower heat stress and dehydration, and minimizes predation pressure from diurnal raptors (Alerstam 1990, Able 2001). Predominantly diurnal migration is relatively rare in passerines, having been documented in only a few families, including Corvidae, Sturnidae, Hirunindiae, Fringillidae, and some Icteridae (Evans and Rosenberg 2000, Able 2001, Evans and O’Brien 2002).

Detecting the specific identity of nocturnally migrating birds is largely limited to two techniques: (1) scavenging birds killed during night migration at radio towers, lighted buildings, and other human made structures, and (2) identifying species by listening to or recording their flight calls. Many migratory songbirds produce flight calls, a primary vocalization given during sustained flight. Flight calls are prevalent among North American passerines, although not all species produce them. For example, species of Tyrannidae, Laniidae, Vireonidae, Troglodytidae, and Mimidae are not known to give flight calls but are nocturnal migrants (Evans and O’Brien 2002, Farnsworth 2005). Passerine flight calls are typically between two and 10 kHz and <1 sec in duration (Ball 1952, Evans and O’Brien 2002). Flight calls, like songs and other calls, are species-specific, varying in frequency, duration, modulation, and pattern among taxa (Farnsworth and Lovette 2005). Flight calls are theorized to maintain flock stability (Hamilton 1962) or spacing by communicating information among migrating birds in close proximity to each other (Thake 1981). Flight calls were first documented in 1899 when Orin Libby detected over 3,000 flight calls in a single night (Libby 1899). Advances in spectrographic analysis and inexpensive recording devices (Evans 1994, Farnsworth 2005) and, especially a well-documented catalog of flight calls that allows identification of most species (Evans and O’Brien 2002), have made it possible to identify species and document their temporal and spatial nocturnal migration patterns (Evans and Rosenberg 2000).

Migratory movements of North American species or subspecies of fringillids, although occasionally detected in pre-dawn hours, have not previously been documented in night passage migration (Evans and O’Brien 2002). Both diurnal and occasional nocturnal passage migration have been documented in two European species, Common Chaffinch (Fringilla coelebs) and European Greenfinch (Carduelis chloris) (Clement 1999), and in Greenland and Eurasian subspecies of Common Redpoll (Acanthis flammea) (Knox and Lowther 2000). We document for the first time the apparent nocturnal migration of Pine Siskins (Spinus pinus), a species normally considered a diurnal migrant but whose flight calls are readily distinguishable among the fringillid species.

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METHODS

Waterproof pressure-zone microphones were used to concurrently record nocturnal flight calls from 2 to 16 October 2008 at three locations within 6 km of Gardiner, Maine, USA. Site #1 was at 44° 13' N, 69° 46' W; Site #2 was at 44° 13' N, 69° 47' W; and Site #3 was at 44° 16' N, 69° 47' W. Two microphones were within 2 km of each other and the third was ~6 km distant. Two microphones were in suburban neighborhoods with low level street-light illumination while the third was on the border of an extensive forested area with no artificial lighting. All three locations were within 1 km of the Kennebec River, a major southward flowing river. Each microphone was placed and pointed upwards so that it had an unobstructed path to the sky. Acoustic XLR cable connected the microphone to a Rolls MP13 pre-amplifier housed in a nearby building. The signal was sent from the pre-amplifier into a computer which automatically activated two simultaneously running bird flight call detection software programs (Thrush-r.exe and Tseep-r.exe; both distributed as shareware from www.oldbird.org) at 2000 hrs EST and de-activated the programs by 0600 hrs EST the next morning (the detector programs at one station at times were allowed to continue slightly past 0600 hrs EST). Each potential bird flight call detected by either program was saved as a WAV file with a file name reflecting the date and time it was detected. All sound files collected were reviewed aurally and spectrograms inspected visually using Glassofire sound analysis and file sorting software (distributed as shareware from www.oldbird.org). Non-bird sounds were removed and bird sounds were sorted and saved by date. More detailed spectrographic analysis and measurements were completed using Raven sound analysis software (available from Cornell Laboratory of Ornithology, Ithaca, NY, USA). Flight calls that we considered to be of Pine Siskins because they were identical to the well-known and described "Kdeew" flight call of the species (Sibley 2000), based on our own field experience, were saved and sent to flight call and bird identification experts William Evans, Michael O'Brien, and David Sibley for external review.

RESULTS

We identified 212 of 2,432 flight calls detected at all three stations that we considered likely characteristic of Pine Siskins. Our three expert reviewers independently concurred that 90% of the calls were clearly identifiable as Pine Siskin flight calls. We were left with 190 calls that were confirmed as those of Pine Siskins after removing calls for which there was not consensus among our experts. All flight calls were archived at Macaulay Library of Natural Sounds at Cornell Laboratory of Ornithology (catalog numbers 140388–140396).

Our stations recorded Pine Siskin flight calls from 10 to 16 October 2008 when all three stations were shut down for the season. Calls were detected as early as 2146 hrs EST and as late as 0606 hrs EST (Fig. 1), but detections occurred throughout the night with calls detected in every hour between 2300 and 0600 hrs EST the following morning. Approximately 90% of recorded flight calls were between 0000 and 0500 hrs EST, and ~80% of calls were at least 1 hr before sunrise (Table 1). One hundred and thirty of the 190 recorded calls occurred on 15 October 2008. Recording stopped on 16 October and the full extent of migration dates is unknown.

DISCUSSION

Many species of North American finches thought to be virtually exclusive diurnal migrants, including Pine Siskin, have been recorded producing flight calls in the hour before sunrise as they begin their diurnal migrations (Evans and O'Brien 2002). Flight calls of Pine Siskins were recorded in our study in significant numbers throughout the night over multiple nights and multiple locations, suggesting these birds were likely undergoing nocturnal migration. To our knowledge, this is the first documented observation of apparent nocturnal migration in this species.

The migratory irruptive behavior of Pine Siskins is apparently induced proximately by a lack of food resources, primarily conifer seeds (Dawson 1997). Pine Siskins are known to make long-distance migratory movements biennially on average (Bock and Leptien 1976, Yunick 1983, Hochachka et al. 1999), apparently due to broad scale synchronicity of conifers in their biennial cycle of cone production (Pielou 1988). Birds will not show these long-distance migratory movements when cone production is high in a particular region, while in poor seed production years, large numbers will move in search of food (Dawson 1997).

Nocturnal migration could be a behavioral trait that is only expressed by finches under extreme conditions.
conditions of food shortage which induce long-distance migratory movements similar to those seen in determinate long-distance migrants (Hochachka et al. 1999). There was an unusually large migratory irruptive event for Pine Siskins during the 2008–2009 season, especially in the eastern United States. The average flock size reported by Project FeederWatch participants in the eastern U.S. doubled from the prior year’s migration (7.2 to 15.5), and the number of feeders visited increased by 31% (D. N. Bonter, pers. comm.). Data from eBird across ~480 sites in Maine, New Hampshire, Vermont, and Massachusetts showed a detectable pulse in the frequency of checklists reporting Pine Siskins in the second week of October 2008 from 1.7% in week one to 11.2% in week two and 7.1% in week three (eBird 2010). This pulse corresponded with the period when we detected Pine Siskin night flight calls suggesting that a broad-scale migratory movement of the species was underway across New England. The frequency of 11.2% in the second week of October 2008 was the highest observed for Pine Siskins in October since 2001 (eBird 2010).

Another irruptive cardueline finch that occurs in North America, Common Redpoll, has been heard migrating nocturnally in Greenland and Eurasia (Knox and Lowther 2000), but there are few data on the extent and timing of this behavior. These and our observations suggest this is a rare behavior among finches. Future study of nocturnal migration during irruptive years could help explain if nocturnal migration is a plastic behavior induced under conditions that lead to broad scale

**TABLE 1.** Number of Pine Siskin flight calls detected per night at each of three sites near Gardiner, Maine from 10 to 16 October 2008. Recordings were not made at all sites on all nights, as indicated by “N/A”.

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irruptions in contrast to a seemingly determinate migration strategy as seen in virtually all other passerines.

**ACKNOWLEDGMENTS**

We thank the Tyler and Hynes families for use of their homes as recording sites. We thank the Biology Department at Bates College for funding all travel expenses for M. L. Watson. We also thank W. R. Evans, M. O’Brien, and D. A. Sibley for reviewing our recorded flight calls.

**LITERATURE CITED**


**Orientation of Sap Wells Excavated by Yellow-bellied Sapsuckers**

**Ashley M. Long**

**ABSTRACT.**—Ambient temperature may influence selection of foraging sites by organisms that use sap as a primary food source. I examined the spatial orientation of sap wells excavated by Yellow-bellied Sapsuckers (Sphyrapicus varius) on pine trees (Pinus spp.; n = 43) in eastern Kansas. Sap wells were oriented toward the southwest (α = 246.04°, s = 65.46°, P = 0.004), unlike in previous studies. Benefits of southwesterly sap well orientation may include avoidance of high winds while foraging and increased flow of sap on the sides of trees warmed by afternoon light. Received 2 November 2009. Accepted 25 October 2010.

The Yellow-bellied Sapsucker (Sphyrapicus varius) is a small-medium, migratory woodpecker (21–22 cm) that breeds throughout Canada and portions of the northern United States and
overwinters throughout much of Mexico, the eastern United States, and Canada (Howell 1952, Walters et al. 2002). The Yellow-bellied Sapsucker, like other North American woodpeckers, forages on a variety of foods including fruits and insects; however, sapsuckers are also known to consume sap as a primary food source (Beal 1911, Howell 1952, Tate 1973, Williams 1975, Wilkins 2001, Walters et al. 2002). Sapsuckers in winter and early spring, obtain sap from small, circular wells excavated in the xylem tissue of trees (Foster and Tate 1966, Tate 1973). Wells excavated in phloem tissue of trees are used for foraging during the summer months (Tate 1973, Eberhardt 1994). The placement of sap wells excavated by Yellow-bellied Sapsuckers has been previously studied in relation to preferred tree species (Conner and Kroll 1994, Eberhardt 1994), bark- and phloem thickness (Wilkins 2001), tree health (i.e., fungal infections and wounds from lightening) (Ohman and Kessler 1964, Lawrence 1967), bark moisture (Eberhardt 2000), tree density (Eberhardt 2000), proximity to nest site (Eberhardt 1994), and sucrose content of sap (Kilham 1964, Tate 1973, Wilkins 2001). However, factors that influence spatial orientation of sap wells around tree boles remain unclear.

Observations by Kilham (1956) imply that sunlight and sap flow rates may dictate sap well orientation. He noted that Yellow-bellied Sapsuckers could be observed excavating wells in the morning hours and returning to these wells to feed in the afternoon when sap flow was at its peak. My objective was to ascertain if orientation of sap wells excavated around tree boles in eastern Kansas is nonrandom. I predicted that sap wells would be oriented toward the south-southwest, the side of the tree most exposed to sunlight during daylight hours at this latitude throughout months when sapsuckers are present.

METHODS

I measured the orientation of sap wells (relative to magnetic north; 0°–359°) excavated by Yellow-bellied Sapsuckers in March and April 2008 at five sites in Emporia, Kansas, USA (38° 24' 29" N, 96° 11' 13" W; Lyon County). The study sites were on public property (e.g., city parks) within the city limits of Emporia and were landscaped with a variety of native and non-native deciduous and coniferous tree species generally planted in single, evenly spaced rows to serve as wind blocks around the perimeter of each property. Detailed temperature- (collected from 1971 to 2010) and wind data (collected from 2005 to 2010) were obtained through the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html). Emporia’s average monthly temperatures ranged from 2 to 21° C during the time of year when Yellow-bellied Sapsuckers are present in this region (Oct–Mar; Walters et al. 2002). Average monthly wind speeds for this same time period (i.e., Oct–Mar), ranged from 16.8 to 19.9 kph and average monthly wind orientations (relative to magnetic north) were between 1 and 36°, indicating that prevailing winds are from the north when sapsuckers are present.

Sap wells were identified as small, evenly distributed holes excavated in horizontal lines on tree boles. Other sapsuckers excavate wells in similar patterns, but the Yellow-bellied Sapsucker is the only sapsucker species known to overwinter in this region. Sap well orientation was measured as the direction of highest sap well concentration when ≥10 sap wells were observed on a single tree. I estimated the area of highest sap well concentration as the side of the tree bole containing ≥50% of the sap wells excavated and recorded sap well orientation from the center of the sap well cluster. No distinction was made between newly- and previously excavated wells due to uncertainties regarding time since sap well excavation. I also measured the diameter at breast height (DBH; cm) and distance from ground to sap well cluster (m) for each tree where sap well orientation was recorded.

Mean DBH, mean distance from ground to sap well cluster, and their associated standard deviations were calculated. Analyses for circular distributions (Zar 1999) were used to examine mean orientation (d) and circular standard deviation (s) of sap wells excavated by Yellow-bellied Sapsuckers. I used Rayleigh’s test of uniform distribution to examine if sap well orientation was nonrandom (Zar 1999). Approximate P-values were obtained using 5,000 permutations and macros created for the SAS system (SAS Institute Inc. 2003) by Kölliker and Richner (2004). The alpha level for Rayleigh’s test was set at 0.05.

RESULTS

Sap wells excavated by Yellow-bellied Sapsuckers were observed exclusively on pine trees (Pinus spp.) at the study sites. Thirty-eight percent of the pine trees examined (n = 114) contained evidence of foraging by Yellow-bellied Sapsuck-
FIG. 1. Orientation (relative to magnetic north; 0–359°) of sap wells excavated by Yellow-bellied Sapsuckers on pine trees (Pinus spp.) \((n = 43)\) in eastern Kansas. Bars along the radial axes indicate the number of trees within 30° intervals.

ers and a sufficient number of sap wells to ascertain the orientation of the sap well cluster. Tree species foraged upon included Austrian pine \((P. nigra; n = 3\) trees), red pine \((P. resinosa; n = 2\) trees), and white pine \((P. strobus; n = 38\) trees). Average DBH was \(37.87 \pm 13.78\) cm \((SD)\) and average distance from ground to sap well cluster was \(1.16 \pm 0.48\) m \((SD)\). Sap wells were not randomly distributed around tree boles and exhibited a significant southwesterly orientation \((\bar{a} = 246.04°, s = 65.46°, P = 0.004; \text{Fig. 1})\).

DISCUSSION

Observed patterns of nonrandom sap well orientation on pines in eastern Kansas may be a result of Yellow-bellied Sapsucker avoidance of the northern side of tree boles, rather than selection of the southwestern side. Trees foraged upon by this species in this region of the United States are often planted as single row wind breaks, greatly exposing foraging sapsuckers to high velocity winds from the north during the winter months. Benefits of southwesterly sap well orientation may include decreased metabolic stress (i.e., fewer calories burned and/or reduced probability of desiccation) or increased perching stability as a result of wind avoidance.

Exposure to solar radiation can result in significant temperature differences between exposed and shaded sides of trees (Derby and Gates 1966). More optimal foraging opportunities exist for sap feeding organisms that select feeding sites where ambient temperature or solar radiation positively influence the rate of sap flow (Goldingay 1987, Howard 1989, Pejchar and Jeffrey 2004). Pejchar and Jeffrey (2004) found that the Akiapolaau \((Hemignathus munroi)\), an endangered endemic species of Hawaiian Honeycreeper that uses similar foraging techniques as sapsuckers, feeds preferentially on ohia \((Metrosideros polymorpha)\) trees on slopes that receive the greatest intensity of sunlight and, therefore, have the highest rates of sap flow. Yellow-bellied Sapsuckers in eastern Kansas may similarly
benefit from increased sap flow on the sides of trees most exposed to sunlight during daylight hours at this latitude.

Secondary benefits of increased sap flow may also exist. This species feeds primarily on sap, but they are also known to forage on insects that congregate near sap wells (Foster and Tate 1966, Tate 1973). Sapsucker foraging opportunities on arthropods may increase along with greater sap-foraging opportunities if insects are drawn to sunlight during the cooler days of early spring. However, there is little evidence supporting the idea that insects have a dominant role in orientation of sap wells, as other studies report few insects around wells during the winter months (Wilkins 2001); it has been suggested that sapsuckers may perceive insects in close proximity to sap wells as competitors rather than prey (Walters et al. 2002).

My research indicated a pattern of southwestern sap well orientation, but other studies examining the distribution of sapsucker wells on tree boles found sap well orientation to be oriented to the north (Varner et al. 2006) or random (Wilkins 2001). In the southern United States where these studies were conducted, sap flow may be less influenced by ambient temperature and tree exposure to wind may be greatly reduced. The significant southwest orientation of sap wells in this study, and lack thereof in other studies, may be a result of variation in solar angle, wind speed, and wind direction, in addition to physiological differences among tree species used by foraging sapsuckers. Future research regarding this topic should examine latitudinal variation in sap well orientation and the influence of tree physiology on sapsucker foraging behavior.

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LITERATURE CITED


ABSTRACT.—We report observations of the Austral Parakeet (*Enicognathus ferrugineus*) feeding on larvae in the northern part of its distribution in the austral temperate forests of Argentine Patagonia during the pre- and post-reproductive seasons. Larvae consumed were *Aditrochus fagicolus* (Chalcidoidea: Pteromalidae) in leaf galls of *Nothofagus pumilio* (79 observations), larvae from Homoptera, Lepidoptera, and Diptera in seed galls of *N. pumilio* (12 observations), and larval Nemonychidae (Coleoptera) in male cones of *Araucaria araucana* (69 observations). Our observations suggest *Enicognathus ferrugineus* could be more insectivorous than previously thought, perhaps to help meet their demand for high-quality food during the pre- and post-reproductive seasons. Received 3 December 2009. Accepted 8 October 2010.

Temperate birds apparently time breeding to coincide with annual peaks in food availability as food can be an important limiting factor, especially in habitats with sharply defined cold and warm seasons (Newton 2003). Breeding behavior involves a large parental investment prior to the laying period, when birds search for high-quality food to attain adequate physiological condition (Krebs and Davies 1993).

Parrots (Psittaciformes) are generally known for being mostly seed-eaters (Collar 1997), but their diet can vary depending on the habitat. Parrots breeding in temperate forests experience a markedly seasonal environment where protein-rich food (important during pre-breeding stage; Martin 1987, Koutsos et al. 2001) is scarce prior to summer, and is limited primarily to pollen and nectar, which become available in late spring (Díaz and Kitzberger 2006), or larvae (Moorhouse 1997). Protein requirements are high for nestlings and females with large broods (Koutsos et al. 2001). Parrots with large broods inhabiting temperate habitats must find an extra protein supply before and during the reproductive season, just when protein rich-foods may be most scarce.

The Austral Parakeet (*Enicognathus ferrugineus*) is restricted to Andean temperate forests in Patagonia from 36 to 54° S (southern Argentina and Chile; Collar 1997), and information on its biology, ecology, and population status is scarce. Given their extreme southern distribution, the lack of knowledge about their adaptations to the austral climate highlights the importance of understanding their ecological and reproductive requirements. Pairs breed once per year; laying starts in December (late spring) and nestlings fledge in March (late summer). Broods are large with respect to body size with females laying between five and eight eggs (Collar 1997). Only anecdotal data concerning the bird’s ecology (mainly diet and breeding aspects) were available prior to 2001. Leaves, flowers, fruits and seeds, and occasionally larvae comprise its known diet (Forshaw 1989, Collar 1997, Díaz and Kitzberger 2006). Díaz and Kitzberger (2006) report that diets of Austral Parakeets in lenga beech (*Nothofagus pumilio*) forest varied seasonally, following forest phenology and availability of food resources. The diet of the Austral Parakeet includes buds and pollen from lenga beech and its hemiparasite *Misodendrum* in the pre-reproductive period, leaves of both species and seeds of *Misodendrum* during the reproductive season; and lenga beech seeds during the first part of the post-reproductive season. Food becomes scarce as winter approaches, and their diet is then comprised of low nutritional food such as *Cyttaria* spp. fruit bodies and buds. We found sporadic intake of larvae was more frequent than previously known and report observations of these unusual feeding habits of this species.

OBSERVATIONS

We conducted field research from 2007 until 2009 designed to document the basic foraging behavior of the Austral Parakeet in an Argentine mixed lenga beech and pehuen (or monkey puzzle tree) (*Araucaria araucana*) forest (hereafter MF).
within the northern part of the Austral Parakeet's distribution (37° S, 71° W) near the Chilean border at 1,050 m elevation. Feeding behavior of Austral Parakeets from a southern location was also recorded during November–December 2005, 2008, and 2009 in a pure old-growth Nothofagus pumilio forest (hereafter PF) at 41° S, 71° W; 1,300 m elevation.

Observations were made while systematically walking along human and animal trails, covering the entire study area between 0800 and 1100 hrs in the morning (720 hrs in MF and 288 hrs in PF). We recorded the exact location each time a parakeet or flock was detected, and the identity of food items consumed to species level. If the parrots changed to another food source during the period of observation, the new material was recorded as a different feeding bout (Galetti 1993). Each feeding bout varied from a few seconds to several minutes with the entire flock participating in each observation.

Flocks of five to 39 birds were observed within MF on 43 occasions during November and December eating Aditrochus fagicolus (Chalcidoidea: Pteromalidae) larvae (Nieves-Aldrey et al. 2009) in lenga beech leaf galls. Additionally, we recorded occasional consumption of lenga leaf galls 36 times during November–December in 2005, 2008, and 2009 in PF. Flocks of between 60 and 80 individuals were seen eating the contents of leaf galls, always in the same PF patch within each of the 3 years. We observed 221 Austral Parakeets (flocks between 4 and 7 birds) during December between 2007 and 2009 in MF on 69 different occasions eating larvae of Nemonychidae (Coleoptera) inside male pehuen cones. Austral Parakeets were observed 12 times (136 individuals in flocks of 8–11 birds) eating lenga beech seed galls (Mar–Jun 2008 and 2009). These galls housed insects in the Orders Homoptera, Lepidoptera, and Diptera. The parakeets ate only the larvae and discarded the vegetative parts of the gall (lenga beech leaf and seed galls) or pehuen male cone in all cases.

DISCUSSION

Consumption of larvae was mainly concentrated during the pre-reproductive period (92.5% of the observations), indicating synchronization between demand for high-quality food, and the sporadic and concentrated appearance of galls and cones. Food availability in MF throughout the pre-reproductive period (Dec) of Austral Parakeets is relatively low and primarily consists of pollen of 10 different species (SD, unpubl. data). Austral Parakeets were selective during this period and only consumed lenga beech, pehuen, and Misodendrum pollen. All observations of Austral Parakeets foraging on larvae contained within male pehuen cones were obtained during this period. These cones take half a year to complete their development and are hard to open while green. December, when the pollen is released, is the only time of the year when the male cones are fully developed and easy for Austral Parakeets to open and take advantage of the opportunity to forage on them. Larvae develop partially inside the cones until the cones are mature and fall from the trees, making them unavailable to parakeets. There are no observations of Austral Parakeets feeding on male cones or larvae contained within them once they have fallen to the ground. Lenga beech leaf gall consumption was also concentrated in the pre-reproductive period in both locations. Parakeets consumed mature and immature galls, which are distinguishable by their color, suggesting that larvae of different sizes were ingested. Parakeets were not observed to feed on larvae or insects during the reproductive season, when alternative sources of food were more available. The parakeets fed primarily on leaves and seeds (SD, unpubl. data for MF; Diaz and Kitzberger 2006 for PF) during this period.

The consumption of larvae contained in lenga beech seed galls was only observed during the post-fledging period, when almost all lenga beech seeds are mature. These larvae may represent an important protein source for juveniles as the seeds are available until winter (SD, unpubl. data), and lenga beech seeds have only 12% protein and 19% lipids (Diaz and Kitzberger 2006). This suggests post-reproductive events, including juvenile dispersal and molting, rather than nesting, coincide with a short period of elevated protein-rich food availability.

Adult arthropods infest galls and cones in a locally aggregated way (e.g., stand of trees) (J. L. Nieves-Aldrey, pers. comm.). Parakeets appear to know the precise location and timing of this food source, because they used it year after year in the pre-reproductive season. Thus, Austral Parakeets maximize exploitation of ephemeral protein sources during the period of high nutritional demand that occurs after winter scarcity.

Forshaw (1989) indicated parrots are far more insectivorous than generally suspected. Insects are
common in the diet of some Australian parrots, including Major Mitchell's Cockatoo (Lophochroa leadbeateri) (Rowley and Chapman 1991), Western Corella (Cacatua pastinator) (Smith and Moore 1991), and New Zealand Kaka (Nestor meridionalis septentrionalis) (Moohouse 1997), as well as Rüppell's Parrot (Poicephalus rueppelli) (Selma et al. 2002), but only when other food is scarce.

The consumption of arthropods by neotropical parrots may be more common and widespread than previously thought. Seasonal variations in diet with occasional ingestion of adult insects and spiders have been noted for some species (Galletti 1993, Wermundsen 1997). Diptera larvae have been found in stomach contents of Blaze-winged Parakeet (Pyrrhura devillei) (Moojen et al. 1941) and Peach-fronted Parakeet (Aratinga aurea) (Schubart et al. 1965). The Painted Parakeet (Pyrrhura picta) has been reported extracting and eating arboreal termites from their nests (de Faria 2007). Cockle et al. (2007) reported Vinaceous-breasted Amazons (Amazona vinacea) presumably foraging on caterpillar larvae during a severe drought. Aramburu and Corbalán (2000) detected several arthropod species in the stomach contents of nestling Monk Parakeets (Myiopsitta monachus monachus) of nestling Monk Parakeets (Myiopsitta monachus monachus) presumably from preening ectoparasites. It seems less common for psittacids to consume larvae from leaf galls, although such larvae constituted 6.6% of the diet of Lilac-crowned Amazons (Amazona finschii) (Renton 2001) and were consumed daily for at least 2 weeks by a group of Maroon-bellied Parakeets (Pyrrhura frontalis) (Martuscelli 1994).

Our results suggest the Austral Parakeet is more insectivorous than previously thought. They inhabit temperate forests with marked seasonal shortages of food which may have led them to occupy a broader dietary niche than other parrots by supplementing their intake of high-quality food, such as pollen (Diaz and Kitzberger 2006), during the pre- and post-reproductive season with novel items such as insect larvae.

ACKNOWLEDGMENTS

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LITERATURE CITED


ABSTRACT.—Foraging associations between birds and other groups of animals have been widely reported in the literature. I report the first observation of a foraging tactic involving a flock of Greater Ani (Crotophaga major), which deliberately followed fish along an artificial ditch in the Pantanal wetlands, feeding on animals flushed by the movement of the vegetation on the ditch banks. Further observations of the feeding behavior and foraging tactics of Greater Anis are necessary to ascertain if this type of behavior is a frequent event or merely sporadic.

Commensal foraging associations, where individual foraging opportunities are enhanced by actions of other unaffected individuals, are well known in nature and there are a relatively large number of reports in the scientific literature (King and Cowlishaw 2009). Birds are one of the groups most frequently studied as many species have the capacity to forage by catching prey flushed from a variety of substrates by other terrestrial animals (Willis and Oniki 1978, Dean and MacDonald 1981, Roberts et al. 2000). Among the best known associations of commensal foraging are those between birds and army ants (Oniki and Willis 1972, Willis and Oniki 1978, Willis 1983). During their sorties, ants moving in large numbers disturb a variety of insects and other small animals, which become potential prey for birds (Willis and Oniki 1988). Similarly, birds have been observed catching prey flushed by a wide variety of animals including primates (Fontaine 1980, Boinski and Scott 1988, Siegel et al. 1989, Ferrari 1990, Warkentin 1993), white-nosed coatis (Nasua narica) (Booth-Binczik et al. 2004), nine-banded armadillos (Dasypus novemcinctus) (Komar and Hanks 2002), maned wolves (Chrysocyon brachyurus) (Silveira et al. 1997), ungulates (Heatwole 1965, Dean and MacDonald 1981, Källander 1993), and other birds (Baker 1980, Robbins 1981).

Reports also exist that involve birds in foraging associations with aquatic animals. These accounts come from observations in marine environments where birds were observed foraging in association with cetaceans (Au and Pitman 1986, Camphuysen et al. 1995, Camphuysen and Webb 1999, Santos et al. 2010), pinnipeds (Rieder 1957), tuna (Au and Pitman 1986), and stingrays (Kajura et al. 2009). These marine animals, during their hunting forays, frequently confine their prey close to the surface to facilitate capture; these aggregations attract seabirds that dive to feed (Martin 1986, Camphuysen and Webb 1999, Clua and Grosvalet 2001). However, I found no reports of foraging associations involving birds and freshwater animals.

The Greater Ani (Crotophaga major) ranges from northern Argentina to Panama in South America; it typically occurs along riverbanks with vegetation and in gallery forests, flooded areas,
marshlands, and mangrove swamps (Payne 1997, Sick 1997). Greater Anis are gregarious and live in groups of four to >100 individuals (Hilty and Brown 1986) foraging on arthropods and small vertebrates from mid-canopy to the ground. They occasionally venture into the forest, usually to follow army ant columns (Willis 1983, Hilty and Brown 1986). I describe the first record of a commensal foraging association involving a flock of Greater Anis and freshwater fish, based on an opportunistic observation along a man-made waterway in the northern region of the Pantanal, Brazil.

STUDY AREA

The Pantanal of Mato Grosso is the plain formed by the upper reaches of the Paraguay River and its tributaries in western Brazil, in the states of Mato Grosso and Mato Grosso do Sul with a small portion in Bolivia and Paraguay. The plain slopes gently in the region creating a complex system of river flooding and ebbing with slow run-off (Antas 2004). This annual cycle of flooding and ebbing in the Pantanal has caused local residents to depend upon boats for transport during the rainy season, as well as in flood and ebb periods when roads are impassible. Boat transport during the latter two periods, when travel by road is difficult, has been enhanced by digging ditches parallel to roads to retain sufficient volume of water for use of boats, extending their use before and after the peak of the rainy season. These ditches have been dug to facilitate transportation of materials and people to and from the (RPPN) ‘Private Natural Heritage Reserve’ SESC Pantanal. The RPPN SESC Pantanal is in the northern Pantanal (16° 41' 11" S, 56° 10' 32" W) in the municipality of Barão de Melgaço, State of Mato Grosso and covers an area of 106,782 ha. Digging of one of the ditches began in 2002 and it is cleared every year during the dry season to remove the accumulation of vegetal material. The ditch is ~2 m wide with a depth of between 0.5 to 1.5 m.

OBSERVATIONS

At ~0800 hrs on 3 February 2007, a group of nine Greater Anis was observed moving along a ditch for about 20 min. The anis were foraging close to the water’s edge, catching insects amid the riverbank vegetation. Throughout this observation, the group stayed within ~1–2 m of each other, moving at a constant pace (~1 m every 10 sec). From a vantage point, ~30 m distant, I observed the anis were catching insects that flushed from vegetation emerging from the water that was being disturbed by fish that were darting back and forth along the edge of the ditch. The water surface remained calm and without current, allowing partial view of fish that were closer to the water surface. At times I noticed the fish performed more abrupt movements, such as a fight, when I could see many insects flushed by the movement of vegetation. All anis in the group foraged along the ditch, including five young (short tail, opaque plumage, bill not yet hooked, dark irises). The birds eventually dispersed, probably due to an approaching boat.

DISCUSSION

This is the first account of which I am aware involving birds and freshwater fish in a commensal foraging association. However, there are reports in the literature of commensal foraging behavior that involve Greater Anis associating with army ants (Willis 1983), as well as groups of monkeys (Cebus spp.) and Hoatzins (Opisthocomus hoazin) (Sigrist 2006). Fish may congregate in the shaded waters of riverside galleries to take advantage of the remains of fruit and insects that fall on to the water surface (Sigrist 2006), thus providing opportunities for birds to forage on the insects flushed by the activities of fish at the surface. It has been shown for some species of birds that visual orientation is of great importance in catching prey (Eriksson 1985). However, it is unlikely in the present account that the birds focused their foraging based on the presence of fish, due to the turbidity of the water. It is more likely the birds detected the movement of the vegetation and the resulting movement by potential prey. The frequency of this type of opportunistic behavior by Greater Anis, and birds in general, may be low in relation to broader foraging tactics. The paucity of reports involving birds and freshwater fish suggest it may be sporadic. However, I believe this event can occur more frequently in the late ebb, when the flooded area decreases and concentration of fish increases. Further observation of the feeding behavior and foraging tactics of Greater Anis is necessary.

ACKNOWLEDGMENTS

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Adoptions of Young Common Buzzards in White-tailed Sea Eagle Nests

Ivan Literak\(^1,3\) and Jakub Mraz\(^2\)

ABSTRACT.—Documentation of interspecific adoption of young is rare in the published literature among birds. We survey six cases of young Common Buzzards (\textit{Buteo buteo}) adopted in nests of White-tailed Sea Eagles (\textit{Haliaeetus albicilla}) in central Europe (Czech Republic and Hungary). Common Buzzard nestlings adopted were in good condition and adult White-tailed Sea Eagles fed and cared for them properly. Young Common Buzzards successfully fledged and left the White-tailed Sea Eagle nests. The most probable explanation of this phenomenon is a non-lethal predation of Common Buzzards followed by White-tailed Sea Eagle parental care as a result of parental recognition error. Similar cases of adoption of Red-tailed Hawk (\textit{Buteo jamaicensis}) nestlings in nests of Bald Eagles (\textit{Haliaeetus leucocephalus}) have been documented in North America.

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Adoption is defined in the ornithological literature as caregiving to young or eggs by unrelated adults but interspecific adoption has rarely been reported (Capck et al. 2000). Repeated cases of the same type of interspecific adoption have been described only in nesting Bald Eagles (\textit{Haliaeetus leucocephalus}) in North America which adopted young Red-tailed Hawks (\textit{Buteo jamaicensis}) (Stefanek et al. 1992, Watson et al. 1993, Watson and Cunningham 1996). We observed adoption of a Common Buzzard (\textit{B. buteo}) nestling in a White-tailed Sea Eagle (\textit{H. albicilla}) nest in the Czech Republic in 2007. In addition, we found notes about other such cases in the Czech Republic and Hungary in the local literature, suggesting this type of interspecific adoption by raptors is probably more frequent in central Europe than we had supposed. We report cases of adoptions of young Common Buzzards by nesting White-tailed Sea Eagles and speculate on possible explanations for this phenomenon.

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**OBSERVATIONS**

We originally observed a young Common Buzzard reared in a nest of White-tailed Sea Eagles near the village of Hrachoviste, southwestern Czech Republic (48° 55' N, 14° 46' E). The nest was in a forest close to a clearing and was built on a Scots Pine (\textit{Pinus sylvestris}) tree at a height of ~20 m. The nest was checked by the second author on 20 May 2007 to see if the young eagles were at an age suitable for ringing. There were two eagles ~3 weeks of age and, surprisingly, also a live Common Buzzard chick ~2 weeks of age. All young were in good condition. Adult eagles were flying above the nest and an adult Common Buzzard also was observed flying above the nest but it was not evident whether this individual could be a parent of the young buzzard in the eagle nest. The nest was checked again on 12 June 2007 during which time the young buzzard had already fledged and was sitting in a tree at a distance of ~150 m. The two young eagles (~6 weeks of age) stayed on the nest. This proved that adult White-tailed Sea Eagles from this nest had adopted a young Common Buzzard and cared for it during a period of at least ~3 weeks. No adult Common Buzzard was observed near the nest during the second visit. The second author personally checked 21 nests of White-tailed Sea Eagles in the Czech Republic and found a young Common Buzzard only in the nest described.

**DISCUSSION**

A young Common Buzzard was observed in 2000 by P. Kurka in the nest of a White-tailed Sea Eagle in the northern part of the Czech Republic (Schropfer 2002). P. Kurka was checking the nest on a pine tree on 4 June 2000 and found one young White-tailed Sea Eagle and one young Common Buzzard both alive, as well as two dead young Common Buzzards ~1 week of age. No more information is available for this case. A nest of White-tailed Sea Eagles with two Common Buzzard chicks of different ages plus a White-tailed Sea Eagle nestling was found in Hungary in 2007.
All three young successfully fledged and left the nest. Three more cases in which young Common Buzzards were found in White-tailed Sea Eagle nests originated also from Hungary (Palko 1997, Fenyosi and Stix 1998, Horvath 2006).

Interspecific brood parasitism, placement of nestling hawks in eagle nests by humans, and non-lethal predation followed by parental care have been considered as causes of this phenomenon for young Red-tailed Hawks adopted in Bald Eagle nests in North America (Stefanek et al. 1992, Watson et al. 1993, Watson and Cunningham 1996). Interspecific brood parasitism has not been recorded in the Accipitridae (Yom-Tov 2001), and this scenario was considered unlikely for the cases of adopted nestlings of Red-tailed Hawk (Stefanek et al. 1992, Watson et al. 1993). We support this contention regarding the cases of adopted nestlings of Common Buzzards in nests of White-tailed Sea Eagles. For brood parasitism to have occurred, Common Buzzard females would have had to enter the eagle nests, contend with an adult White-tailed Sea Eagle with newly hatched nestlings, and laid its eggs. The eggs would have had to be incubated by the adult eagles, the eagle nestlings or both. White-tailed Sea Eagles begin to nest (lay eggs) in central Europe in February and incubation lasts 34–46 days. Common Buzzards begin to nest at the end of March and incubation lasts 33–35 days. There is no tendency among Common Buzzards for brood parasitism and the time difference between the start of nesting for both species makes brood parasitism improbable. Thus, we do not believe brood parasitism is a realistic explanation of these phenomena.

The most plausible explanation for these phenomena is non-lethal predation followed by parental care. This scenario was considered the more likely explanation for the occurrence of live young Red-tailed Hawks in Bald Eagle nests (Stefanek et al. 1992, Watson et al. 1993, Watson and Cunningham 1996), and we suggest the same explanation for cases in which young live Common Buzzards occurred in White-tailed Sea Eagle nests. One of the adult White-tailed Sea Eagles may have captured the nestling Common Buzzard as prey for its own nestlings and failed to kill it during capture and transport. Food-begging calls of Common Buzzard chicks that survived the transport apparently stimulated feeding from the White-tailed Sea Eagles (Horvath 2009). The adopted Common Buzzards were usually in good condition with no apparent signs of abuse by the adult or nestling eagles. It suggests the adult eagles fed them properly and/or the Common Buzzards were able to scavenge sufficient food to stay alive and fledge. Corroborating this hypothesis is information that birds, including chicks from nests of Grey Herons (Ardea cinerea), commonly occur in White-tailed Sea Eagle diets (Balat and Belka 2005, Belka and Horal 2009, Horvath 2009). The presence of raptor species also was found in an analysis of Bald Eagle prey items collected at nests in the USA (Stefanek et al. 1992). Moreover, raptors at times bring prey that is still alive to their nests (Spofford and Amadon 1993). In addition to Red-tailed Hawks in Bald Eagle nests, another case of an apparent nonlethal predation was a Glaucous-winged Gull (Larus glaucescens) chick and subsequent adoption by a pair of Bald Eagles as noted in Alaska (Anthony and Paris 2003).

The adoption of Common Buzzard chicks by White-tailed Sea Eagles could be explained as a parental recognition error because there are no benefits for parents to adopt chicks of an unrelated species. The Common Buzzard nestlings benefited, however, from the recognition error of the eagles. The White-tailed Sea Eagle and Bald Eagle, as are non-colonial bird species, are probably unable to distinguish their offspring from other species (Alcock 1997). We consider this type of adoption as a surprising phenomenon in central Europe. Numbers of nesting pairs of White-tailed Sea Eagles in the Czech Republic and Hungary were relatively low; they numbered ~50 and 180 nesting pairs in the Czech Republic and Hungary in 2007, respectively (Belka and Horal 2009, Horvath 2009). Conversely, the Common Buzzard is the most common raptor species in this area and the last census for a nesting population in the Czech Republic revealed 11,000–14,000 nesting pairs (Stastny et al. 2006).

We consider noteworthy that this phenomenon of interspecific adoption occurs in raptors with similar ecological niches in both North America and Europe. The Bald Eagle is a North American ecological equivalent of the White-tailed Sea Eagle, and the Red-tailed Hawk is among the most common raptors in North America just as the
Common Buzzard is in Europe (Thiolley 1994). Mixed broods of Red-tailed Hawks and Bald Eagles in the USA occurred at a frequency of 0.5% (3 of 662) of eagle broods observed during 1987–1991 (Watson et al. 1993). Our data are presently too limited to calculate a frequency of adoptions of Common Buzzards in White-tailed Sea Eagle nests in Europe.

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LITERATURE CITED


Cruise Ships as a Source of Avian Mortality During Fall Migration

Carol I. Bocetti1,2

ABSTRACT.—Avian mortality during fall migration has been studied at many anthropogenic structures, most of which share the common feature of bright lighting. An additional, unstudied source of avian mortality during fall migration is recreational cruise ships that are brightly lit throughout the night. I documented a single mortality event of eight Common Yellowthroats (Geothlypis trichas) on one ship during part of one night in fall 2003, but suggest this is a more widespread phenomenon. The advertised number of ship-nights for 50 cruise ships in the Caribbean Sea during fall migration in 2003 was 2,981. This may pose a significant, additional, anthropogenic source of mortality that warrants further investigation, particularly because impacts could be minimized if this source of avian mortality is recognized. Received 27 October 2009. Accepted 23 August 2010.

Mortality during migration of neotropical migratory songbirds is an important topic to bird conservationists. Anthropogenic causes of mor-
Avian mortality during fall migration has been attributed to multiple anthropogenic structures, including vehicles, communication structures, buildings and windows, powerlines, and wind turbines (Erickson et al. 2001). Avian mortality during migration has also been documented at offshore oil derricks (Hope-Jones 1980) and at navigational lightships (Bullis 1954). The common element among most of these sources of avian mortality is lighting. The bright lights may attract night-migrating birds (Gauthreaux and Belser 2006, Gehring et al. 2009). An additional source of modern avian mortality during fall migration is impact and death by exhaustion on the open decks of recreational cruise ships.

**OBSERVATIONS**

On 28 September 2003, while aboard a 14-story, 3,114-passenger cruise liner in the Caribbean Sea (~80 km south of Miami, Florida, USA), I observed a massive, mixed-species flock of migratory songbirds and egrets flying around the ship. Flock size could not be estimated due to the erratic, non-directional flight behavior of the flock, but a visual snapshot would suggest the flock was in the magnitude of thousands. During a 45-min sweep (0015 to 0100 hrs, EDT) of parts of the open area of two decks, I found eight dead Common Yellowthroats (Geothlypis trichas). The mortality was due to impacts with glass windows of upper decks (based on location of two carcasses directly below windows) and exhaustion from flight within the wind drafts of these open decks (4 deaths witnessed). Many birds were trapped within partially enclosed portions of these decks. The most common species observed within these partial enclosures was the Common Yellowthroat. Other species observed resting on the ship included Louisiana Waterthrush (Parkesia motacilla), American Redstart (Setophaga ruticilla), Tree Swallow (Tachycineta bicolor), and Barn Swallow (Hirundo rustica). Cattle Egrets (Bubulcus ibis) were observed flying around the ship, but they did not land on the vessel. Cattle Egrets were likely preying upon the aggregated flock of songbirds (P. W. Sykes Jr., pers. comm.), adding an additional source of mortality. It appeared the birds were attracted to the lights of the ship, and then became confused and caught in the wind draft associated with the ship's movement (~22 knots/hr).

The weather condition was overcast with air temperature ~23°C. About 3 hrs prior to the observation period, it rained hard for about 1.5 hrs. Migrants may have lowered the altitude of their migratory path due to weather conditions of that evening. However, songbirds were observed in partially enclosed portions of the ship during the daytime of the previous 4 days. The weather conditions of preceding nights were clear skies with similar air temperatures, suggesting the rain event was not what brought the songbirds into close proximity of the ship. Egrets were also observed flying in the wind draft of the ship on three previous nights, during clear sky conditions. Unfortunately, I did not visit the open decks or watch carefully for songbird migrants on any of the other nights during the cruise.

Considering that in 2003 there were ~50 large cruise ships that carry 1,200 or more passengers operating in the Caribbean Sea (with destinations in the Bahamas, East Caribbean, South Caribbean, West Caribbean, and East coast of Mexico only) during the fall migration (Aug–Oct), this source of avian mortality may not be trivial (Table 1). These ships are advertised as 207 to 311 m in length, and are 10–14 stories in height. They are all well lit at night. The general design of these vacation cruise ships is to have 3–5 decks with open areas, a few of which have partial enclosures. On the ship I observed, the area I searched covered ~1/4th of the open areas on the ship, excluding balconies (wind draft of ship does not swirl into these areas). My 45-min observation period represented ~1/15th of the dark hours of the night. To extrapolate from the mortality I directly observed (4 deaths, excluding the 4 birds that were found already dead); this single ship on this single night may have resulted in four bird deaths × 4 × 15 = 240 bird deaths. The cleaning staff of the cruise ship acknowledged removal of songbirds from the deck during early morning hours prior to guest activities, although they did not admit how often or how many dead birds were removed. Based on advertised sail dates and itineraries, the 50 large (>1,200 passengers) cruise ships operating in the Caribbean Sea during August through October result in an estimated 2,981 ship-nights (Table 1). Assuming 240 bird deaths per ship-night, an estimated 715,440 bird deaths may have occurred on large cruise ships in the Caribbean Sea during fall migration 2003.

Given the small sample size and low sampling intensity, I am uncertain whether the mortality I
TABLE 1. Cruise ship companies and number of large (>1,200 passengers) ships (and ship-nights*) sailing in the Caribbean Sea during fall migration (Aug-Oct) 2003.

<table>
<thead>
<tr>
<th>Cruise ship company</th>
<th>Number of ships</th>
<th>Number of passengers</th>
<th>Speed (knots)</th>
<th>Number of ship-nights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Royal Caribbean</td>
<td>11</td>
<td>2,020–3,114</td>
<td>19–22</td>
<td>777</td>
</tr>
<tr>
<td>Carnival</td>
<td>17</td>
<td>1,452–2,974</td>
<td>21–22</td>
<td>1,267</td>
</tr>
<tr>
<td>Princess</td>
<td>6</td>
<td>1,950–2,600</td>
<td>284</td>
<td></td>
</tr>
<tr>
<td>Celebrity</td>
<td>5</td>
<td>1,354–1,950</td>
<td>21–24</td>
<td>148</td>
</tr>
<tr>
<td>Holland America</td>
<td>5</td>
<td>1,266–1,848</td>
<td>22–24</td>
<td>134</td>
</tr>
<tr>
<td>Norwegian Cruise Line</td>
<td>4</td>
<td>1,748–2,400</td>
<td>21–25</td>
<td>147</td>
</tr>
<tr>
<td>Disney Cruise</td>
<td>2</td>
<td>1,750</td>
<td></td>
<td>224</td>
</tr>
<tr>
<td>Totals</td>
<td>50</td>
<td></td>
<td></td>
<td>2,981</td>
</tr>
</tbody>
</table>

* Ship-night = sum of advertised nights of all cruises for all ships of each company.

observed is representative of a typical fall night. I assumed the estimated kill for the single ship-night on 28 September was representative of the entire fall migration season simply to produce an approximate estimate of avian mortality to begin considering the impact of this additional anthropogenic structure. I also assumed the ship I observed was representative of other large ships. I only included large ships (>1,200 passengers) in my estimate of ship-nights to strengthen that assumption. Many smaller ships also sail the Caribbean during the fall season, but their deck arrangement and lighting patterns may be different from the larger cruise ships.

**DISCUSSION**

The Caribbean Sea is crossed by millions of neotropical migrants every fall. The decline of many of these species is of significant conservation concern. Perhaps even more alarming is the known presence of the endangered Kirtland's Warbler (Dendroica kirtlandii), the entire population of which must cross these waters during fall migration to reach wintering areas in the Bahamas.

This issue warrants further investigation given the multitude of anthropogenic sources of avian mortality during fall migration and the additive nature of this mortality (Erickson et al. 2001). At a minimum, proper studies designed to estimate the magnitude and species composition of avian mortality on cruise ships during the fall migration period are warranted. Studies should address species-specific causal factors including light attraction, weather conditions, time of day, and time of year.

Efforts to work with the industry to minimize impacts would be prudent. If studies show lights are attracting birds, it is possible that alternative lighting options for these ships could reduce the impact on migratory birds. For example, light covers could prevent the light from illuminating skyward. This may eliminate the attraction to overhead migrating birds. Also, the wavelength of the light bulbs could be changed to be less attractive (Gauthreaux and Belser 2006). Flash pattern could also be manipulated to minimize attraction to night-migrating birds (Gauthreaux and Belser 2006, Gehring et al. 2009). Finally, most lights could be completely turned off after 0200 hrs when the ships’ daily activities are terminated. This could reduce by half the number of night-lighted hours on the ship.

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**LITERATURE CITED**


First Record of Aplomado Falcon (Falco femoralis) for the West Indies

Blake A. Mathys

ABSTRACT.—I report the first sighting of Aplomado Falcon (Falco femoralis) for Puerto Rico and all of the West Indies. I observed a single individual at Laguna Cartagena National Wildlife Refuge (southwestern Puerto Rico) on 15 January 2008; the individual stayed until 25 January 2008. Photographs establishing the bird’s identity were obtained during prolonged periods of observation by several observers. Received 30 January 2010. Accepted 4 August 2010.

The Aplomado Falcon (Falco femoralis) occurs from the southern United States, through Central America, to Argentina in South America. It is generally sedentary, although individuals in the extreme northern and southern part of the range are partially migratory (Keddy-Hector 2000). It is a medium-sized falcon (200 to 500 g), and primarily preys on birds and insects, although small mammals and reptiles are also taken (Keddy-Hector 2000). The Aplomado Falcon occurs in open habitats including grasslands, savannahs, and prairies. It has not been previously recorded on any Caribbean island (excluding Trinidad, which is biogeographically South American; Raffaele et al. 1998). I report the first record of this species for the West Indies.

OBSERVATIONS

I observed an Aplomado Falcon on 15 January 2008 at Laguna Cartagena National Wildlife Refuge (18°01’ N, 67°06’ W) in southwest Puerto Rico. I was observing West Indian Whistling Ducks (Dendrocygna arborea) on the southwest side of the refuge. I scanned several dead trees for a Peregrine Falcon (Falco peregrinus) that I had regularly seen in the area. At 1320 hrs (AST) I saw a raptor, smaller than a Peregrine, perched in one of the dead trees on the northwest shore of the lagoon at a distance of ~400 m. It was observed through a 60X spotting scope. I immediately recognized it as an Aplomado Falcon, due to the long tail, dark vest-like coloration on the chest, and pronounced light stripe over the eye. I was familiar with this species, having previously seen multiple individuals in Venezuela and Mexico. It stayed at this perch for ~25 min, spending most of the time preening. I took special care to observe the legs to look for bands or jesses, clues to probable captive provenance. The left leg was completely free of any objects. The bird then flew directly toward me, eventually landing in larger trees ~65 m to the west of the observation tower. I later returned to these trees to look for the falcon. It flushed from the trees, circling a few times before landing again in a tree ~10 m from me. I was able to closely observe both legs and confirm there were no bands or jesses on either. It was also at this perch that I obtained the best photographs by “digi-scoping” with a four megapixel digital camera through the ocular lens of my spotting scope (at 20X). The bird flushed and flew to the west, and later flew east of the observation tower and roosted at the top of a tree. I observed it later in the afternoon on the north side of the lagoon perched on fence posts and at the tops of trees.

The Aplomado Falcon was seen frequently over the next 10 days, generally on the north side of the lagoon. I left Puerto Rico on 20 January, last personally seeing the falcon at 1100 hrs on 19 January. It was well photographed by Mike Morel on 21 January, and last reported on the morning of 25 January by Maria Camacho and Eduardo Ventosa.

DISCUSSION

I identified the bird as an Aplomado Falcon during the initial observation on 15 January 2008 as I was familiar with the species in Mexico and Venezuela. Peregrine Falcon, Merlin (Falco columbarius), and American Kestrel (F. sparverius) were observed at Laguna Cartagena on most days, and it was immediately obvious due to size and well-defined marking that the falcon was not any of the expected species.

Other physically similar falcon species including Bat Falcon (F. rufgularis), Orange-breasted Falcon (F. deiroleucus), and Eurasian Hobby (F.
subbuteo) were considered and rejected as candidates during the initial viewing. Bat Falcon would be most likely having been recorded as a vagrant to Grenada (Raffaele et al. 1998). The Bat Falcon, a species I have seen multiple times in Venezuela and Mexico, is smaller with a shorter tail and full dark hood, the latter character especially being quite different from the distinctive facial pattern of the Aplomado Falcon. The bird was first seen perched on a dead tree that a Peregrine Falcon had been frequenting. It appeared slightly smaller than a Peregrine Falcon, therefore much too large to be a Bat Falcon. The distinct black vest, combined with the light supraclavicular stripe and dark facial markings, clinched the identification. The long, banded tail was observed well during the bird’s preening, a character with which I had been particularly impressed while previously observing Aplomado Falcons in Venezuela. Australian Hobby (F. longipennis) can be eliminated due to lacking a dark vest and not showing a complete supraclavicular stripe (Ferguson-Lees and Christie 2005). In addition, its range is geographically distant from Puerto Rico. Lanner Falcon (F. biarmicus), similarly unlikely based on range, can also be eliminated by lack of a dark vest, shorter tail, and less distinct supraclavicular stripe when present (Ferguson-Lees and Christie 2005).

There are three subspecies of Aplomado Falcon: F. femoralis septentrionalis and F. femoralis femoralis are geographically the best candidates for a vagrant to Puerto Rico. The other subspecies, F. f. pinchinchae, is geographically distant and shows a much richer rufous coloration than the bird observed. The nominate subspecies is geographically the closest to Puerto Rico.

I was able to observe the falcon for ~8 hrs over 5 days. It was perched on fence posts or small trees (<7 m tall) for the majority of this time. Its observed hunting style was similar to a female Merlin that I observed daily at the lagoon. This Merlin successfully captured dragonflies, and the Aplomado Falcon’s prey items were assumed to be similar. However, no specific prey items were identified.

This species is rare in Central America south of Mexico. It was first recorded in Honduras and Costa Rica during the last 30 years (Koford et al. 1980, Marcus 1983). It is rare in Trinidad, although breeding has been recorded (ffrench and ffrench 1966, ffrench 1991). The closest stable breeding population is in Venezuela, ~800 km south of Puerto Rico.

ACKNOWLEDGMENTS

I thank many Puerto Rican birders for sharing their sightings with me, especially during the period after I left. Sergio Colón, Mike Morel, Manuel Cruz, and Fred Schaffner all communicated sightings and misses toward the end of the falcon’s stay. I also thank the National Geographic Society Committee for Research and Exploration (Grant #8261-07), for providing all of the funding for my research in Puerto Rico. My advisor, J. L. Lockwood, was instrumental in encouraging my work in Puerto Rico.

LITERATURE CITED


Idle Lobster Traps Kill Blue Jays

Mason H. Cline1,3 and Joanna L. Hatt2

ABSTRACT.—We report observations of Blue Jay (Cyanocitta cristata) mortality in idle lobster traps stored on Merepoint Neck in the Town of Brunswick, Maine. Three of nine individual Blue Jays found inside the traps were alive but emaciated. Each of the live Blue Jays was seen picking off and swallowing pieces of pectoral muscles from Blue Jay carcases also inside the traps. We could not find literature describing or warning of the attractive nuisance posed to birds by improperly stored fishing gear, such as lobster traps. Our observations identify a previously undocumented threat to local bird populations, and likely the first documentation of adult-adult cannibalism for the Blue Jay. We suggest some simple solutions to mitigate avian mortality due to improperly stored fishing gear. Received 22 June 2010. Accepted 9 October 2010.

It is widely known that idle and derelict fishing gear cause unintended mortality to marine organisms (Macfadyen et al. 2009). However, we found no documentation describing the threat that idle fishing equipment poses to terrestrial organisms, such as passerine birds. Until this report, idle and improperly stored fishing gear has not been acknowledged as a real and serious threat to survival of terrestrial birds. We describe observations of inadvertent trapping and subsequent mortality of a terrestrial songbird, the Blue Jay (Cyanocitta cristata), in idle fishing equipment.

We also document adult-adult cannibalism by Blue Jays. Reports of adult-adult cannibalism in wild birds are uncommon. Generally, in wild birds, cannibalistic behavior is thought to be the product of either extreme aggression or opportunistic nutritional exploitation (Stanback and Koenig 1992). Conversely, reports of captive birds exhibiting cannibalistic behavior are fairly common. Cannibalism by captive birds is often cited as the product of social and environmental stresses associated with captivity (Duncan and Hawkins 2010).

OBSERVATIONS

Observations were made during a Christmas Bird Count on Merepoint Neck in the Town of Brunswick, Maine. On 3 January 2010 at 0930 hrs EST, while surveying for birds at a public boat launch near the southern terminus of Merepoint Neck, we noticed ~80 metal lobster traps stacked in a rectangular formation. The lobster traps were on property adjacent to the public boat launch. Upon closer inspection, we detected three live Blue Jays caught in three separate lobster traps. The birds could enter the traps, but once inside they were unable to escape. The trapped Blue Jays were initially observed through binoculars from a distance of ~50–75 m. During our initial observation, we noticed a number of Blue Jay carcasses within the lobster traps, in addition to the three live birds. Furthermore, the trapped Blue Jays were observed tearing off and swallowing flesh from the dead Blue Jays.

We approached the traps to extract the live birds. Two of the live individuals had pieces of Blue Jay muscle tissue on their bills. In hand, all three live jays appeared to have reduced muscle mass and felt abnormally bony and light. Upon release, two jays flew strongly while one was noticeably weak and barely able to fly. After the live birds were freed, we carefully examined the six carcasses remaining in the traps. We noted the pectoral muscles of the carcasses were absent and there was no evidence of the missing muscle tissue in the traps or on the snow around or beneath the traps.

Our direct observations of live birds swallowing conspecifics’ muscle tissue coupled with an absence of pectoral muscle tissue on the snow around the traps (which would have been clearly visible on the white background), provides unambiguous evidence for adult-adult cannibalism by the Blue Jay. Displacement behavior has been documented for Blue Jays (Jones and Kamil 1973), but we did not observe this behavior. If displacement behavior had been occurring, we believe that plucked-off and discarded flesh would have been visible in or around the traps.
It is uncertain whether the Blue Jay mortality was due to starvation, hypothermia, antagonistic interactions, or a combination of these factors. Blue mussels (Mytilus edulis) and pieces of fish, possibly from a species of clupeid, were also inside the traps. We did not see the jays consuming these items, but believe this lobster bait likely attracted them to the traps.

DISCUSSION

Little consideration is given to the influence of inactive fishing gear on survival of terrestrial organisms, such as passerine birds. Conversely, the effects of derelict fishing gear on marine organisms are well documented (Dayton et al. 1995). We did not find literature addressing capture and subsequent mortality of terrestrial birds in idle fishing gear. This lack of acknowledgment is perhaps surprising since devices similar to traditional lobster traps have been used to capture landbirds for decades (Weaver and Kadlec 1970). Information concerning the prevalence of this phenomenon and its potential effect on terrestrial bird populations would be valuable to avian conservation efforts.

More than 3 million lobster trap tags were issued in the State of Maine in 2009 (Maine Department of Marine Resources 2010). This figure accounts for the number of traps currently authorized to harvest lobsters in Maine, but certainly underestimates the total number of traps present in the state, most notably unused traps. If even a small fraction of lobster traps are stored in a way that attracts, captures, and kills terrestrial birds, the resulting mortality could influence local bird populations.

This is likely the first documentation of cannibalism by Blue Jays in addition to the conservation implications of our observations. Reports of filial cannibalism exist for the family Corvidae (Richter 1965, Balda and Bateman 1976). However, a search of the ornithological literature yielded no evidence of adult-adult Blue Jay cannibalism and only one record in which adult corvids consumed the flesh of another conspecific adult (Andersen 2004).

This observed behavior of Blue Jays ingesting the tissue of adult conspecifics was probably the product of a high-stress situation. The observed birds were previously wild and became captive. Confined in traps without food, the Blue Jays faced both starvation and social stress. Given this context of captivity and our observations of the emaciated live birds, the motivation for intraspecific predation appears to be, mainly, nutritional. Wild-caught birds held in captivity in previous reports of cannibalism in non-corvids were provided food and water ad libitum. Social stresses (e.g., high densities, lack of necessary stimuli) were cited as causes of cannibalism in these cases (Rodenburg and Koene 2007). The social stress of captivity may have had a role in inducing the Blue Jays we observed to cannibalize, but we believe, based on the poor body condition of the birds, nutritional stress was a major reason for cannibalism.

We argue that improper storage of lobster traps and other fishing gear poses a serious risk to certain local passerine species, especially during periods of low food availability. Simple and inexpensive solutions exist to minimize bird capture, stressed behavior (e.g., cannibalism), and mortality in inactive fishing traps. Thorough removal of bait would prevent luring of birds to stored traps. Elimination of residual bait is especially important if trap storage occurs during periods when food for terrestrial birds is limited. During times of low food availability, birds are more likely to seek out new or additional food sources. Method of storage could also be used to discourage Blue Jays and other species from entering idle traps. Fishing traps stored indoors will not attract birds. Entrance funnels of traps stored outdoors should be obstructed, thus preventing unintended capture of terrestrial birds. Traps could also be covered (e.g., with a tarpaulin) to further protect against inadvertent trapping. These simple precautions would minimize capture of birds and situations of extreme nutritional stress in which birds may exhibit cannibalistic behavior, and would aid in conservation of local bird populations.

ACKNOWLEDGMENTS

We thank two anonymous reviewers. We also thank W. Donald Hudson Jr. for organizing the Christmas Bird Count for Brunswick, Maine and Brittany B. Cline for encouraging preparation of this manuscript.

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Mobbing of Common Nighthawks as Cases of Mistaken Identity

Jeffrey S. Marks,1,5 C. Scott Crabtree,2 Dedrick A. Benz,3 and Matthew C. Kenne4

ABSTRACT.—We report five instances of small birds mobbing Common Nighthawks (Chordeiles minor). In each case, the nighthawk was roosting in a tree during daytime and was mobbed by a group of birds in a manner typical of that directed toward an avian predator. We found only four previously published accounts of perched caprimulgiforms being mobbed. Mobbing birds probably mistake caprimulgiforms for owls because of convergence in plumage coloration and pattern between these two groups of crepuscular-nocturnal birds. Received 29 September 2010. Accepted 9 December 2010.

Most species of “typical” owls (Strigidae) and nightjars (Caprimulgidae) have variegated brown, black, gray, and white plumage that helps provide camouflage for individuals at nests and roosts (Cleere 1998, Marks et al. 1999). Many owls prey on small birds and are frequently mobbed by them (Aldman 1956, Gehlbach and Leverett 1995). In contrast, nightjars feed almost exclusively on aerial insects and are not normally targeted by mobbing birds, presumably because they pose no threat to them. We describe five instances in which a Common Nighthawk (Chordeiles minor) was mobbed by a group of small birds. We also review the scant literature on mobbing of perched caprimulgiforms, none of which appears in the most recent reviews of caprimulgiform biology (e.g., Poulin et al. 1996; Cleere 1998, 1999, 2010). The behavior probably results from similarities in plumage between caprimulgiforms and owls.

OBSERVATIONS

On 23 August 1998, at 1330 hrs MST, JSM encountered a group of warblers mobbing a Common Nighthawk perched on a horizontal limb about 7 m high in an ash tree (Fraxinus sp.) in the town park at Scobey, Montana. During the next few minutes, the warblers gave chip notes, flicked their wings, and hopped from branch to branch <1.0 m from the nighthawk, always facing it while they mobbed. The group consisted of at least 10 Yellow Warblers (Dendroica petechia), two Blackpoll Warblers (D. striata), and two American Redstarts (Setophaga ruticilla). The warblers did not strike the nighthawk, which was oriented parallel to the branch and made no obvious movements in response to the mobbing birds. The warblers departed from the tree in <1.0 min, while the nighthawk remained on its perch. JSM later found several other perched nighthawks in the park that were not mobbed while he was present.

On 4 August 2001, CSC heard mobbing calls...
from a stand of trees near Owings Mills, Maryland, and found a perched Common Nighthawk being mobbed by a group of birds that included several juvenile Eastern Bluebirds (Sialia sialis) and a Pine Warbler (Dendroica pinus), Prairie Warbler (D. discolor), Black-and-white Warbler (Mniotilta varia), Canada Warbler (Wilsonia canadensis), and Baltimore Oriole (Icterus galbula). After about 2 min, CSC accidentally flushed the nighthawk; the mobbing birds flew but did not pursue the nighthawk. About 15 min later, CSC encountered another group of birds vigorously mobbing a second perched nighthawk in the same manner as the earlier observation, although he did not record the species composition of the group. The mobbers exhibited typical behaviors of hopping from branch to branch within 1 m of the nighthawks, giving scolding calls, and flicking their wings, but they did not strike either nighthawk.

On 19 September 2007, at 1600 hrs CST, DAB heard scolding calls as he walked along a road near Winona, Minnesota. He looked up and found a Common Nighthawk perched on a horizontal branch above the road, surrounded by a group of mobbing birds that consisted of a Downy Woodpecker (Picoides pubescens), an Eastern Phoebe (Sayornis phoebe), two Eastern Bluebirds, and a Magnolia Warbler (Dendroica magnolia). A passing car flushed the nighthawk, which flew from view. The mobbing birds immediately dispersed as well.

On the morning of 25 August 2009, MCK spotted a Common Nighthawk perched on a dead branch in a maple tree (Acer sp.) near Algona, Iowa. Shortly thereafter a Black-capped Chickadee (Poecile atricapillus) landed nearby and mobbed the nighthawk. It was soon joined by six more chickadees and a Black-and-white Warbler. The birds mobbed for several minutes and then flew away. The nighthawk remained on its perch the entire time.

DISCUSSION

We found only three previous accounts of a perched nightjar being mobbed. Pickwell and Smith (1938:212) reported that “8 or 10 English Sparrows and 6 robins were noted mobbing an Eastern Nighthawk (Chordeiles minor) as it sat lengthwise on an elm tree...on May 12, 1927.” Ficken et al. (1967) watched five Carolina Chickadees (Poecile carolinaensis), five Tufted Titmice (Baeolophus bicolor), two Blue-gray Gnatcatchers (Polioptila caerulea), and 10 warblers of four species mobbing a Chuck-will’s-widow (Caprimulgus carolinensis) that was perched in a tree. The mobbing lasted ~10 min, during which the nightjar did not change its posture. More recently, Kent (1999) observed a group of about 40 small birds mobbing a Common Nighthawk in Iowa on 30 August 1999. Mobbing species included Northern Flicker (Colaptes auratus), Downy Woodpecker, Blue Jay (Cyanocitta cristata), Black-capped Chickadee, Tufted Titmouse, White-breasted Nuthatch (Sitta carolinensis), American Robin (Turdus migratorius), Gray Catbird (Dumetella carolinensis), eight species of warblers, Northern Cardinal (Cardinalis cardinalis), and Rose-breasted Grosbeak (Pheucticus ludovicianus); the mobbing behavior lasted ~10 min. In each case, the authors suggested the mobbers mistook the nightjar for an owl.

Castro-Siqueira (2010) watched a Common Potoo (Nyctibiis griseus) in central Brazil being mobbed by three Rufous Horneros (Furnarius rufus), two Great Kiskadees (Pitangus sulphuratus), and seven Chalk-browed Mockingbirds (Minis satuninus) for 15 min before the mobbers left the tree in which the potoo was perched. The same group of mobbing birds returned in 5 min and resumed mobbing the potoo; less than 5 min later they were joined by three horneros, two kiskadees, a Tropical Kingbird (Tyrannus melancholicus), and a Rufous-collared Sparrow (Zonotrichia capensis), each of which mobbed the potoo for another 10 min. None of the mobbers struck the potoo, which remained motionless on its perch during both mobbing bouts. Castro-Siqueira (2010) considered the mobbers to mistake the potoo for an owl but cast doubt on that notion because a Burrowing Owl (Athene cunicularia) that was perched in plain view 20 m from the potoo was not mobbed.

Owls and caprimulgiforms have converged in evolving cryptic plumage and thus resemble one another, at least superficially. We agree with Pickwell and Smith (1938), Ficken et al. (1967), and Kent (1999) that this resemblance at times causes small birds to mistake perched caprimulgiforms for owls and mob them accordingly. An alternative hypothesis is that nighthawks and potoos are mobbed because they resemble Chuck-will’s-widows, which occasionally prey on birds (Thayer 1899, Owre 1967). We cannot reject this hypothesis but consider it unlikely because birds that mobbed the potoo in Brazil and
the nighthawk in Montana would not overlap in range with a Chuck-will's-widow at any time of year. Mobbing of a nighthawk, potoo, or any other strictly insectivorous caprimulgiform in either scenario would be a case of mistaken identity. The scarcity of published observations of caprimulgiforms being mobbed suggests the behavior is uncommon. The topic is worthy of attention because it could reveal new information on mobbing behavior, predator recognition, and interactions among caprimulgiforms and other birds.

ACKNOWLEDGMENTS

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LITERATURE CITED


Observation of Ground Roosting by American Crows

Cory M. Shoemaker1,2 and Richard S. Phillips1,3

ABSTRACT.—Communal winter roosts of American Crows (Corvus brachyrhynchos) often occur in urban areas and may number in the thousands of individuals. We documented the distribution of urban roosts of American Crows in central Ohio and, on 12 January 2010, we observed a roost of ~2,500 individuals with ~250-300 birds roosting on the ground. The ground roosting birds remained stationary for the entire observation period of ~45 min indicating this location was not a stopover site. This behavior may increase thermoregulatory benefits during cold nights assuming decreased predation threats in urban environments. We suggest urban ground roosting behavior by crows may be adaptive in colder environments. Received 16 February 2010. Accepted 11 November 2010.

Communal roosts of nonbreeding birds have been the subject of study across taxa. Possible factors driving communal roosting are threefold: protection from predation, informational purposes such as relaying food locations, and potential thermal benefits (Beauchamp 1999). Communal winter roosts of corvids have been documented for several species (Everding and Jones 2006, Zmihorski et al. 2010). The increasing occurrence of corvid roosts in human-dominated landscapes and the potential impact of disease transmission.
have led to increased attention of urban roosts (Ward et al. 2006).

American Crows (Corvus brachyrhynchos) roost communally during the winter, often forming flocks of >1,000 birds (Emlen 1938, Stouffer and Caccamise 1991). Winter roost dynamics of American Crows in North America have long been the focus of study (Caccamise et al. 1997, Preston 2005). Despite efforts to dissuade urban roosting behavior of crows (Gorenzel and Salmon 1992, Avery et al. 2008), studies throughout the range suggest urban winter roosts and habitat associations are becoming more common (Gorenzel et al. 2000, Marzluff et al. 2001). However, why crows may exhibit strong winter roost site fidelity and the mechanisms of winter roost selection remain elusive (Fiedler 1969, Gorenzel and Salmon 1995). Early studies suggest congregation of roosts in Ohio may be impacted by temperature and wind (Haase 1963). Crow roosts have consisted of both deciduous and coniferous trees as well as artificial structures including buildings and bridges (Stouffer and Caccamise 1991, Gorenzel and Salmon 1995, Gorenzel et al. 2000). Examination of winter roosts of American Crows has occurred for over a century (Edwards 1888) but, to our knowledge, ours is the first published observation of urban ground roosting behavior by the American Crow.

**OBSERVATIONS**

We observed American Crows roosting on the ground in Springfield, Ohio on the evening of 12 January 2010 during a study examining patch-occupancy in urban winter crow roosts. Springfield is a city of ~60,000 people in the Miami Valley region of southcentral Ohio. Average winter temperatures range from -7 to 1°C. The crows observed were part of a larger roost estimated at 2,500 individuals discovered during an ongoing study of urban winter roost selection. At 2015 hrs EST, 2.45 hrs after sunset, we noticed a roost on the roof of a public library building and in nearby trees. Temperatures reached a low of -12°C before midnight with winds up to 79 km/hr reported by the National Weather Service in Dayton. Road surface temperatures in areas susceptible to hazardous road conditions ranged from -8 to -16°C overnight according to DOT records (Clark County, Ohio Department of Transportation, pers. comm.).

We noticed roosting birds on neighboring structures and adjacent trees. The site was illuminated by numerous street lights and was bordered by industrial and office buildings. Six streets and an active railroad track bisected the site and crows were observed roosting in parking lots near these roost structures. Approximately 15 cm snow was on the ground but the parking lot had been cleared of snow. Drifting snow had covered about 50% of the lot. A combined total of 250-300 crows was ground roosting in three separate parking lots. Each roost had small trees (DBH <25 cm) bordering the ground roost site with additional birds roosting in these trees.

Most birds in the roost showed little response to human activity (i.e., cars driving by, people walking nearby, and a train passing within 25 m of the roost). Ground-roosting birds remained stationary for the duration of our observation (~45 min) with most birds exposing as much surface area as possible to substrate in what may be described as a resting or roosting position. The presence of crows was not confirmed the following morning, but the stationary nature of the crows, their lack of response to human activity, the length of the observation, and the time frame with respect to sunset, all suggest this was not an observation of a staging event.

**DISCUSSION**

Studies suggest American Crows may be deriving substantial benefit from close association with humans. American Crow populations in urban areas achieve higher densities and experience more rapid population growth yet costs in terms of survivorship and reproduction may be insufficient to explain this growth (Marzluff et al. 2001). Despite winter roosts in northern latitudes, crows do not possess major physiological modifications for existence in cold winter climates other than large body size and possible benefits afforded through nasal feathers (Wunder and Trebella 1976). The available evidence suggests thermoregulation may be a driving factor in American Crow foraging decisions during temperatures below an estimated lower critical temperature (Kilpatrick 2003). Our observations occurred well below estimated lower critical temperatures based on metabolic studies of other corvids, and could provide insight into the potential benefits of urban associations at northern latitudes. Possible thermoregulation benefits from potential wind shelter and heat conductance from the pavement may explain why crows roosted on the ground when trees were available. The road
temperatures recorded were warmer than the air, potentially leading some individuals to roost on the ground in spite of potential increased predation risk. The anecdotal nature of our report requires caution, but we suggest future studies examining urban roost selection by crows evaluate not only structural features but thermal features as well. A better understanding of roost selection criteria may better inform management directed at winter roosts in urban environments.

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LITERATURE CITED


EARLY TASMANIAN ORNITHOLOGY: THE CORRESPONDENCE OF RONALD CAMP-BELL GUNN AND JAMES GRANT 1836–1838. Nuttall Ornithological Club Memoir 16. Edited by William E. Davis Jr. 2009: 263 pages, 30 figures. ISBN 1-877973-47-5. $37.50 (cloth).—William E. Davis Jr. has edited and the Nuttall Ornithological Club has published a small gem of ornithological history. It gives unusual insight into what it must have been like to try to identify birds before the days of well-written regional books and field guides.

Some 180 years ago, Van Diemen’s Land (now Tasmania, Australia’s island state) was sparsely settled and little explored ornithologically. It was at that time that Ronald Gunn, a public official, and James Grant, a physician, began to produce for eventual publication a list of Tasmanian birds. Each had a private collection of birds, owned many of the books then available, and was an avid and very serious amateur ornithologist. A serious drawback to their efforts was that most of the information in their books was brought together by European authors who had never seen the birds alive and whose descriptions and hand-colored plates were frequently less than helpful. At best, reference was to mainland Australian forms. Each of these authors arranged the species in widely varying taxonomic sequence and with disparate ideas of relationships.

In 1836–1838, Gunn, the better-known of the two, was a magistrate in Circular Head in northwestern Tasmania. Davis provides a most welcome biographical sketch of Gunn, who had a long career in public service and was a pioneer of natural history study in Tasmania. Grant was a physician in Launceston, northeastern Tasmania, about whom little is known. During these 2 years, they corresponded regularly and sent specimens back and forth, discussing identifications and relationships of the birds they collected. At various times Gunn also sent specimens to Sir William Hooker in Scotland and to John Edward Gray in London, perhaps for identification, although there is no information in the correspondence that this was provided.

Davis has published the Gunn-Grant correspondence verbatim, interspersed with modern identifications of the birds and page references with frequent commentary on the contemporary references they used. These additions make accessible correspondence that would otherwise prove cryptic to today’s readers.

The outlook of these unsung Tasmanian ornithologists was surprisingly modern. Not only did they wish to publish a list of Tasmanian birds; they also wanted to incorporate into it the natural history information they had gathered by watching birds in the field. Even though their work predated Darwin’s concept of evolution through natural selection, they (page 3) “flirted in several places with evolutionary ideas,” as observed by Davis.

The Gunn and Grant list unfortunately was never completed. Their correspondence ended when Gunn moved to Hobart and his increased civic responsibilities became very time-consuming, although an incomplete synopsis of their ideas on the taxonomic ordering of birds is dated as late as 1840. This cessation of letters also approximately corresponds to the 1838–1839 visit by John Gould to Tasmania, where he met Gunn, and to the beginning of Gould’s publications on Australian birds. It is known that Gunn provided some notes and specimens to Gould subsequent to his visit.

I recommend this book for the rare glimpse it gives into the early difficulties associated with ornithological research and hope it causes everyone to appreciate the splendid books and field guides available to us today.—MARY LECROY, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; e-mail: lecroy@amnh.org

LOOKING FOR A FEW GOOD MALES: FEMALE CHOICE IN EVOLUTIONARY BIOLOGY. By Erika Lorraine Milam. The Johns Hopkins University Press, Baltimore, Maryland, USA. 2010: 168 pages and 13 figures. ISBN: 978-0-8018-9419-0. $60.00 (cloth).—Charles Darwin, with just a few short sentences in the Origin of
Species, proposed a form of selection to account for morphological and behavioral differences between the sexes within a species: sexual selection. Evolution by common descent quickly gained acceptance, but sexual selection by female choice faced significant skepticism and remained a discredited area of research on the fringe of evolutionary biology until the late 1970s, when it finally received its due as an important mechanism for species formation. So the story goes.

Or does it? In *Looking for a Few Good Males*, Erika Milam seeks to replace what she calls this “eclipse narrative” of loss and recovery with a more complex one that stresses the broader scientific and social context in which sexual selection theory was debated. The result is a carefully researched, fascinating history of rich detail on a part of evolutionary biology that has so far garnered little attention among historians, scientists, and the public. This is a thoughtful book that appeals to anyone with an interest in animal behavior or the uneasy relationship between evolution science and the study of human social relationships.

Milam begins by pinning the discomfort raised by Darwin’s theory of sexual selection upon the threat to human exceptionalism posed by cognitive choice in other animals. Darwin was explicit in *Descent of Man and Selection in Relation to Sex*: when evaluating the extravagant plumages and energetic displays of male pheasants (Phasianidae), for example, female pheasants compared competing males and chose the most beautiful from among them. Anticipating his readers’ discomfort Darwin reassured them that, although some of the lower animals undoubtedly possessed a sense of beauty and actively chose their mates, cultivated man (i.e., white Western man) represented the pinnacle of an evolutionary progression of cognitive ability and aesthetic sense. Man alone was capable of rational choice. Most of Darwin’s colleagues, including Alfred Russell Wallace, co-discoverer of natural selection, rejected both choice and an aesthetic sense in other animals, preferring natural selection for male “vigor” as an explanation for male traits that attracted female attention. Unfortunately, the ladder of evolutionary progress appealed to many 19th and 20th century readers, and framed (and constrained) the debate over sexual selection for years to come.

Milam continues with a description of the state of animal behavior research in the decades leading up to the Second World War. Not surprisingly, much of the focus on sexual selection in Europe during that period centered on the eugenic potential for female choice to improve human populations, although interest understandably faded with the end of the war. Darwin’s attribution of aesthetic sense to animals had largely been abandoned while concerns over the encroachment of animals upon the uniqueness of human cognitive ability remained. Despite excellent work by amateur biologists like George and Elizabeth Peckham (spiders) and William Pyraft (birds) that supported female choice and sexual selection, professional evolutionary biologists increasingly rejected conscious female choice for their mates in favor of physiological reactions to external (male displays) and internal (gonadal sex hormones) stimuli.

Eventually, a critical shift in focus occurred from animal mating behavior as precursor to human behavior (the “ladder” metaphor) to animal mate choice and its effect on the process of evolution. This shift was accompanied by new methods that strove to create experimental conditions that mimicked nature as much as possible, and widened the scope of animal behavior science. Researchers increasingly focused on the role that sexual selection might have in reinforcing or breaking down species boundaries. Some (e.g., Gladwyn Kingsley Noble) reported evidence of female choice, while others (e.g., Lester Aronson), concluded that females mated randomly.

Female mate choice, with the rise of ethology in postwar Britain, was rejected outright in favor of mechanistic models of behavior in which a stimulus (male behavior) overcame female inertia. Ethologists placed critical importance on the genetic basis of behaviors, which they saw as innate, ritualistic responses to environmental stimuli. This idea, coupled with advancements in experimental genetics, enabled animal behaviorists like Claudine Petit and Lee Ehrman to investigate the impact of mating behavior on the genetic dynamics of populations and species. Both found strong evidence for female choice. Nonetheless, prominent evolutionists like Theodosius Dobzhansky and Ernst Mayr continued to discount its importance for speciation. Finally Robert Trivers, in his paper “Parental Investment and Sexual Selection,” interpreted Petit and Ehrman’s results in the light of evolutionary game theory, and demonstrated that mate choice must be widespread as well as critically important for
population dynamics. After the publication of E. O. Wilson’s *Sociobiology* (edited by Robert Trivers), interest in sexual selection surged.

Birds, with their obvious sex differences in plumage and behavior and their anthropomorphic appeal, remained a centerpiece of the debate over sexual selection. British naturalist Edmund Selous concluded from hours of observing wild birds that some animals must choose their mates, as did Julian Huxley from his early work on the courtship behavior of Great Crested Grebes (*Podiceps cristatus*) (although he later rejected that view). Bower birds (*Ptilonorhynchidae*), with their elaborate mating arenas and innate preferences for colorful decorative objects, were invoked for decades by some scientists as proof of conscious animal aestheticism, an idea discredited by Australian ornithologist Jock Marshall. Surprisingly, preeminent ornithologist Ernst Mayr conducted his research on female mate choice not in birds but in *Drosophila* fruit flies; readers might be chagrined to learn of his declaration that “there is not as much difference as you might imagine.”

Despite this rich history of inquiry, the decades separating *Descent of Man* and *Sociobiology* are frequently dismissed by modern biologists as bereft of significant advancements in sexual selection. Milam attributes this narrative of “renewal” of sexual selection and female choice partly to efforts by organizational biologists to reclaim evolution from molecular biologists, whose recent triumphs in biochemistry threatened to monopolize public attention and funding. For Milam, this “eclipse narrative” served to paint evolutionary *organismal* biology as a dynamic field with pressing new questions that could be addressed only in nature, not in the laboratory. Fortunately, the momentum of synthesis cannot be contained, and today Darwin’s second great idea is actively tested by dyed-in-the-wool field biologists and genomic technocrats alike—sometimes, even in tandem.—ELEN ONEAL, Postdoctoral Researcher, Duke University, 125 Science Drive, Durham, NC 27708, USA; e-mail: eo22@duke.edu

**BIRDS.** By Dale Serjeantson. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge, UK. 2009: xxvi + 486 pages, numerous illustrations. ISBN: 978-0-521-86617-0 (hardback); 978-0-521-75858-1 (paperback). $85.52 (hardback); $46.67 (paperback).—It is unfortunate that the title of this book, even with inclusion of the series name, is singularly uninformative. The intention of the volume is to summarize the importance of birds to the field of zooarchaeology. This entails interpretation of avian remains, mostly bones, but also including eggshells, feathers, skin, and other traces found in depositional environments that were created mainly by human activity. The content goes well beyond bones and stones, however, and includes an overview of human/bird interactions that also uses evidence from ancient depictions and writings. The topics cover not just birds as food and sources for bone implements, but also uses of birds for sport (e.g., hawkings), aesthetics (pets, ornaments), ritual and symbolism, and environmental reconstruction. Treatment of some of these subjects is at times perfunctory. The introductory parts include some general information about birds, and mainly deal with zooarchaeological methodology such as ascertaining age and sex, species identification, collecting and recording techniques, the processes by which bones become incorporated in deposits (taphonomy), differential survival of various skeletal elements, and their modification by humans. Much of this is too elementary to be of use to anyone with experience in the field but insufficiently comprehensive for someone with no experience at all.

I began reading this book in the middle, in the chapters on domestication, which gave me a much more favorable impression than I was able to maintain with further reading. It is this section that I hope will prove most useful and informative for ornithologists. An entire chapter is devoted to the “chicken” (*Gallus gallus*), which may originally have been domesticated for cockfighting rather than for meat or eggs. Most intriguing is the increasing evidence for pre-Columbian introduction of chickens into the New World along a Pacific coastal route. Shorter accounts deal with turkeys, geese, ducks—including Muscovy Duck (*Cairina moschata*), pigeon (*Columba livia*), peafowl (*Pavo*), guineafowl (*Numida*), and Scarlet Macaw (*Ara macao*). The accounts include historical and archeological evidence for timing and origin of domestication, and the morphological changes that took place subsequently as a result.

Whereas the background of paleontologists is in biology and geology, most zooarchaeologists receive their training in the cultural milieu of the social sciences, which often imparts a different
mindset and weltanschauung regarding procedures and results, and the treatment of literature. Some insight into the different ways of thinking may be gained by Serjeantson’s characterization of bones brought into a human archeological site by wild animals as “intrusives,” whereas in a paleontological site all the stuff trucked in by humans is “intrusive.” Serjeantson has relied almost entirely on the archeological literature for her sources. A glaring omission that is not mentioned is Pierce Brodkorb’s Catalogue of Fossil Birds (5 parts, 1963–1978). Brodkorb went to great lengths to attempt to include every reference he could find to avian remains in archeological deposits; his Catalogue has to be a much more inclusive source for the zooarchaeology of birds than anything cited by Serjeantson.

Lack of ornithological knowledge has resulted in the commission of some “clangers” of unusual plangency. From page 4 alone we have the following. “Birds evolved from theropod [sic] dinosaurs in the Late Cretaceous era (Feduccia 1999).” Whatever birds evolved from, the divergence took place long before the Late Cretaceous, which is a geological period, part of the Cenozoic Era, and citing Feduccia is seriously misleading because he is by far the most outspoken opponent of the theropod derivation of birds. “Cordata” should be “Chordata.” The Linnean classification was established in the 18th, not the 19th century; the idea that it remained basically the same from then until cladistics and DNA analyses brought about “changes in the accepted relationships between families” is beyond nonsensical, especially considering that the taxonomic family is a post-Linnean concept. Hildegarde Howard did not begin her career studying fossils from Rancho La Brea and then move on to the zooarchaeology of the Emeryville shellmound (page 5). Quite the opposite—the Emeryville study was the topic of her Dissertation. The wings of the Galapagos flightless cormorant are not used for swimming, whereas those of all penguins are, not just the larger ones (page 8). Hummingbirds do not feed only on nectar (page 14). Bitterns (Botaurinae) do not “walk on the surface of water” (page 32). The gizzard is not equivalent to the crop (page 32). The generalization about the presence of a triangular patella in birds (page 29), is invalid as an ossified patella is rare in birds and, when present, its shape is extremely variable.

There are many exceptions to the categorical statement that a “pneumatic foramen of the humerus is characteristic of all flying birds” (page 20). The elements of the skull are probably not all “fully fused at the time of hatching” (page 21) in any bird. The structure “at the bifurcation of the trachea in some waterfowl” (page 21) is not the syrinx. Radiale and ulnare are incorrectly rendered as “radial” and “ulnar” (page 28).

What is described as the major digit (page 29) is actually the first phalanx of the major digit. This is indeed perforated in gulls (and terns) but not in some owls and instead occurs in caprimulgids. The generalization about the presence of a triangular patella in birds (page 29), is invalid as an ossified patella is rare in birds and, when present, its shape is extremely variable. The descriptions of the configuration of the tarsometatarsus in zygodactyl birds are badly confounded (page 30). The tarsal cap of the tarsometatarsus is wrongly termed the “hypotarsus” (page 39). Once the terminology has been straightened out, the statement that the “pelvis becomes attached to the synsacrum in the mature bird” (page 23) is not true for many kinds of birds. Here (and pages 110–111) “pelvis” is synonymous with the “innominate bone” consisting of the fused ilium, ischium, and pubis, whereas synsacrum is used to mean only the fused sacral vertebrae (as in Appendix Fig. 2b, where the rendering is so crude as to be unrecognizable). Elsewhere (e.g., page 24) “synsacrum” is used to indicate what I would call the entire pelvis, that is, both innominates plus the fused sacral vertebrae. The wording of the assertion that the “vertebral column includes two sections which fuse in the adult bird: the notarium and the synsacrum” (page 23), probably is intended to mean that each of those elements consists of fused vertebrae, but almost anyone would interpret the statement as meaning that the notarium and synsacrum are fused to each other, which is never true.

The two sentences (page 21) devoted to directionality in the avian skeleton are of absolutely no use to anyone and do not even mention the schism over anterior/posterior versus cranial/caudal. It is hardly surprising that the coracoid “is one of the elements most superficially distinct from mammal bones” (page 26), considering that mammals do not have a coracoid.

Although the geographical coverage of the book is supposedly worldwide, it is in fact heavily Eurocentric. There is no treatment whatever of
the West Indies. No mention is made of the human/bird interface in the Hawaiian Islands that resulted in the extinction of birds nearly as spectacular and peculiar as those of New Zealand.

As hinted above, poor or idiosyncratic writing hinders communication throughout the book. One of my peeves is the pernicious and often seemingly affected substitution of "which" for "that." Though by no means the only transgressors, the Brits are among the greatest sinners in this practice and Sarjeantson is the worst I have ever encountered. The word "that" has been totally abrogated in this book and is not used, except when utterly unavoidable. The most glaring example is the last sentence on page 19 where "which" appears six times, all but five of which should have been "that" according to the standards of Bernstein (The Careful Writer, 1965). Pronouns with ambiguous or distant antecedents are another cause of poor writing. One has to backtrack through five sentences to discover that the last "it" in the paragraph spanning pages 50-51 refers to medullary bone. Can anyone figure out what the following sentence means? "Ireland has more than one tenth as many records of open ground species and water-birds as Britain and a similar number of woodland birds but fewer than 4 per cent as many records of owls" (page 367). Peculiar turns of phrase are "during the time of lay" rather than "laying" (page 49 and elsewhere), and repeated statements that various kinds of artifacts were made "on" or "from" would normally be used.

The extensive bibliography, although not comprehensive, includes many references that the ornithologist would probably never encounter. Many of these, in addition to being obscure, border on, or fall squarely within, the category of "gray literature," which does not seem to create the kind of discomfort and skepticism among anthropologists that it does for most biologists. There are errors in the bibliography as well. Bickart is consistently misspelled Bickhart here and in the text. At least one reference is glaringly misalphabetized.

To be fair, there is a lot of information in this book that has not been summarized in any other source of which I am aware. The researcher should be forewarned that this information can at times be erroneous or incomplete. Personally, I would not cite any fact from this book without going back to the original literature, which in many cases would probably prove very difficult to do. Nevertheless, the book represents a first source that one may turn to try to get a start on any subject involving avian zooarcheology or the history of human/bird interactions. An expanded and corrected edition would be a primary asset in any ornithological library.—STORRS L. OLSON, Curator Emeritus, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA; e-mail: olsons@si.edu


The well written Introduction is important for a full understanding of the species accounts. This includes sections on Geography and Climate, Flora and Vegetation, and Geographic Divisions and Habitats that provide the basis for the ecological distribution of the birds. A section on the Structure of Ornithology treats key organizations, coordinated fieldwork, and publications, showing how the knowledge of bird distribution and abundance has been developed and is being sustained. Notably lacking in this section is any mention of the great museum collections that provide vouchers for much of the accumulated knowledge. A section on Evolution and Taxonomy emphasizes modern molecular analyses with a discussion of subspecies. There is a thorough section on Migration and Movement, one on Biogeographical Affinities, and a final one on Conservation. Information in all these sections relates to points made in the species accounts. There is a thorough section on Migration and Movement, one on Biogeographical Affinities, and a final one on Conservation. Information in all these sections relates to points made in the species accounts. The carefully selected 86 color photos on 32 pages illustrate points made in the introductory text or in species accounts.

Each species account includes paragraphs on Taxonomy, Distribution, and Status. The first may discuss relationships within the family or genus, and the number of subspecies worldwide, citing evidence from recent morphologic or molecular studies. In a number of instances, however, taxonomic changes suggested by the molecular evidence discussed have not been
implemented. Among many examples, a study suggesting that American Black-billed Magpies (Pica hudsonia) should be separated from those in Europe at the species level is cited but the split is not made. The paragraph on Distribution notes the worldwide range of the species, sometimes with information on habitat and migratory behavior, particularly where the latter is geographically variable.

The paragraph on Status is, as the book title suggests, the heart of the account. For rarer species, there is usually a record of first occurrence in Britain and/or Ireland, and an indication of the number of records with the amount of detail depending on frequency of occurrence. Some interesting tidbits show up, such as the first Wilson’s Phalarope (Phalaropus tricolor) being recorded within ~80 km (50 miles) of the birthplace of Alexander Wilson. The first record of Pallid Swift (Apus pallidus), a museum specimen, was not identified until 75 years after its collection. For more abundant or regularly occurring species, there may be information on the size of populations in various places, including increases or declines over time and probable reasons for such changes. Extensive long-term monitoring studies, discussed in the Introduction, permit detailed analysis for some species, particularly seabirds and waterfowl. The amount of detail in these sections is impressive.

An Appendix provides useful species lists, by subspecies, coded by category of occurrence and origin (native, introduced), for each of four geopolitical areas—Great Britain, Republic of Ireland, Northern Ireland, and The Isle of Man. A second Appendix is a list of species whose occurrence in those islands is believed not to be of natural causes, such as escaped cage birds. There is a wealth of information in this book, probably more than most of us in North America want or need to know about British birds. Actually, it might make us jealous that we don’t know as much about most American birds, or at least don’t have it all in one handy volume. I recommend this book not only as a source of information but as a model of how to present important information. It is a worthy addition to both individual and institutional libraries.—RICHARD C. BANKS, Department of Vertebrate Zoology, National Museum of Natural History, P. O. Box 37012, Washington, D.C. 20013, USA; e-mail: banksr@si.edu

THE BIRDS OF BARBADOS. By P. A. Buckley, Edward B. Massiah, Maurice B. Hutt, Francine G. Buckley, and Hazel F. Hutt. British Ornithologists’ Union Checklist Number 24. 2009: 295 pages, 78 color plates, and 5 line drawings. ISBN: 978-0-907446-29-3. $70.40 (cloth).—An isolated outcrop of coral limestone ~160 km east of the main chain of Lesser Antillean islands, the island of Barbados unsurprisingly hosts a relatively depauperate avifauna for its size, represented by only 30 native breeding species of which only one is endemic, plus one that is extinct and seven introduced species that have become successfully established. As a consequence it may seem odd that a hefty 295-page monograph, the 24th contribution to the British Ornithologists’ Union checklist series, could be dedicated to the birds of Barbados. But what the island lacks in native species is made up for by an astonishingly long list of visitors, migrants, and vagrants due to its unique geographical position in the migratory crossroads between North America and South America, and especially as a landfall for trans-Atlantic vagrants of Palearctic birds—including some that have occurred nowhere else in the Western Hemisphere, which gives Barbados its ornithological fame.

Initiated in 1954 by Barbadian residents Maurice B. Hutt and Hazel F. Branch Hutt, The Birds of Barbados is the long-anticipated culmination of more than half a century of compilation and writing. In 1993 the Hutts invited P. A. Buckley and Francine G. Buckley to join them as coauthors of a growing manuscript and shortly afterward they were joined by Barbadian birders Edward B. Massiah and Martin D. Frost. Unfortunately, the Hutts died before the manuscript was completed, first Hazel in 1997 and then Maurice in 1998, and Frost later dropped out of the project as a coauthor due to other commitments, although his substantial contributions clearly merit his inclusion as a coauthor.

Typical of the BOU’s checklist series, The Birds of Barbados comprises much more than an “annotated checklist.” It is an exceptionally scholarly and detailed summary of not just the island’s avifauna, but also many aspects of its natural history, which partially explains why it took so long for the authors to complete the manuscript. No less than 25 pages are devoted to detailed descriptions of the island’s topography, geology, pedology, climate, weather, winds, freshwater and wetlands, vegetation and floristics, freshwater fishes, amphibians, reptiles, mammals,
human history, and conservation concerns. Surprisingly, the controversial issue of hunting migratory shorebirds—which has become highly publicized in recent years—is relegated to a single paragraph. Five maps illustrate the geographical position of Barbados, its elevation and bathymetry, rainfall, human population density, and land use.

The introductory sections on the island’s natural history are followed by 33 pages of detailed discussions on the avifauna of Barbados. The obligatory sections on ornithological history are followed by a glossary of terms used in the book, highlighted by an informative discussion of the term “vagrancy.” The composition of the avifauna is extensively analyzed and augmented by nine tables. The authors make extensive comparisons between the avifaunas of Barbados, St. Lucia, and the Cayman Islands. However, I think comparisons with nearby Grenada, Trinidad, and Tobago would have been more relevant and interesting. A fascinating panoply of subjects are discussed, including vicariance, dispersal, geographic origins, historical changes (including extinctions and introductions), vagrancy, endemicity, molecular insights on phylogenetic relationships, migration (including radar and mist-net studies), and fossil birds. The authors note the potential role of Barbados as a gateway for Palearctic species colonizing the Western Hemisphere. In 1994 the hemisphere’s first breeding population of Little Egret (Egretta garzetta) became established in Barbados and the authors suggest that increasing numbers of Grey Heron (Ardea cinerea) and Western Reef Heron (Egretta gularis) arriving in Barbados may soon colonize Barbados or nearby regions. A research agenda provides a long list of potential ornithological projects awaiting researchers.

The introductory appetizers are followed by the main course: an annotated account for each of 261 species of birds whose occurrence on Barbados is considered to be adequately documented—plus an additional two species in a “Note added in proof” on page 75. Each species account includes sections succinctly describing its status in the “World,” “West Indies,” and “Barbados,” respectively, plus a “Comments” section. A “Breeding” section summarizes breeding for resident species and the museum acronym is given in a “Specimens” section for any species represented by one or more specimens. Species of dubious occurrence in Barbados are also discussed.

The English names of birds follow the British spelling conventions of F. Gill and M. Wright (2006, Birds of the world: recommended English names, Princeton University Press), but with several exceptions (Appendix 20). Perhaps unsurprising, given the instability of avian taxonomy, the authors have not followed the current species-level taxonomy of the American Ornithologists’ Union’s (AOU) North American Classification Committee and South American Classification Committee. Instead, several taxa recognized as subspecies by the AOU are treated as distinct species, including the North American (Anas carolinensis) and Eurasian (A. crecca) forms of Green-winged Teal, dark and white forms of Great Blue Heron (Ardea herodias), eastern and western forms of Willet (Tringa semipalmata), North American and Eurasian forms of Whimbrel (Numenius phaeopus) and Black Tern (Chlidonias niger), and North American (Dendroica aestivalis) and West Indian (Mangrove D. petechia) forms of Yellow Warbler. Each of these forms has been recorded in Barbados, thus elevating the number of species recorded on the island. The authors appear to be hedging their bets that these forms will all eventually be formally split into separate species by the relatively conservative AOU.

The center of the book includes 40 color plates illustrating maps and habitats, and another 38 color plates illustrate birds, including many excellent documentary photos of vagrants. The back of the book provides 24 appendices, including the number of specimens in each of 12 museums for 112 species (Appendix 22), recovery data for 163 birds of 23 species banded in nine other countries (Appendix 23), and a gazetteer of localities (Appendix 24). A lengthy list of references is followed by separate indices of scientific and English bird names.

The book is an admirable compilation of information on the birds of Barbados, and sets a high standard that will be difficult to eclipse. The authors deserve accolades for their careful scholarship. However, I was frustrated with a few features of the book’s organization. More than six pages near the beginning of the book are devoted to summarizing 12 tables, five figures, and 78 plates, but no page numbers are given. This was unfortunate because the tables are not numbered sequentially and do not always appear near where they are first cited, which makes them difficult to locate. For example, Table 2 appears on page 9 but is not cited until page 31, and Table 12 is cited on page 27 but does not appear until page 74. I could not find any obvious errors in spelling.
although I couldn’t overlook my middle initial appearing as “B” instead of “E” and the surname of my friend Courtenay Rooks being spelled as “Rookes” on page 61. I was also surprised that the middle initial(s) of authors was left out of the Literature Cited section, which hopefully won’t be repeated by researchers who use the book as a source of references.

Although Barbados is unlikely to ever become a prime destination for birders or ornithologists who are more interested in hotspots of endemic species, The Birds of Barbados is an essential resource for anybody who is seriously interested in birds of the eastern Caribbean. Birders who relish searching for and finding vagrants will be especially interested in the book because of its wealth of detail on the occurrence of vagrant species, especially trans-Atlantic Palearctic vagrants, many of which have occurred nowhere else in the Western Hemisphere. Field biologists and amateur naturalists interested in other aspects of natural history in the eastern Caribbean will also find the book useful for its detailed descriptions of the natural history of Barbados.—FLOYD E. HAYES, Department of Biology, Pacific Union College, Angwin Ave-

PHILLIPPS’ FIELD GUIDE TO THE BIRDS OF BORNEO. By Quentin Phillipps, illustrated by Karen Phillipps. Beaufoy Books, Oxford, England, 2009: 369 pages, 141 color plates, 644 range maps, and 7 regional maps. ISBN: 978-1-906780-10-4. $25.00 (paper).—This is the book I wish I had when I first visited Sabah, north Borneo. Upon arrival, I took a bus from the capital, Kota Kinabalu, to Tanjung Aru, a nearby coastal site with a small park featuring casuarinas, palms, pandans, and garden plants. The park was full of pigeons, sunbirds, tailorbirds, ioras, trillers, woodswallows, munias, babblers, and bulbuls, and I had no clue how to identify any of them. With the Phillipps’ book, I could have turned three pages and seen most of the pertinent species illustrated on one lively plate. The same is true for visits to the beach, rice padi, river, or the summit of Mt. Kinabalu, Southeast Asia’s highest mountain; summary plates are provided by the Phillipps for each of these habitats, as well as lowland and montane forest. These plates and a 10-page guide to the island’s natural history sites are two of several features that make the Phillipps’ book a wonderful introduction to the birds of Borneo. But experienced birders and ornithologists need not fear that the Phillipps’ book is an irritatingly incomplete guide for novices. On the contrary, it has a complete set of outstanding plates of the 664 Bornean species, and it also has range maps for all non-migratory (and most migratory) birds on the island. And this is just the beginning.

The Phillipps’ book is not really a field guide; it is a guide to the natural history of birds of Borneo that also happens to be handy for identifying species. There is another newly minted book, Myers (2009), that is an excellent traditional field guide to Bornean birds. It contains all the information expected in a modern field guide for identifying species (Sheldon 2010). The two books complement one another. The Phillipps’ do not bother with bird descriptions; instead, they emphasize general information on bird biology, habitat characteristics, and ornithological anthropology. This information makes the book much more interesting to read than a field guide. Lots of information is provided for each species on occurrence, behavior, song, and nesting, but much of the really good stuff appears outside the species accounts. For example, each group of birds is introduced with an extensive paragraph that often features unexpected insights, e.g., tailorbirds (Orthotomus) secure their sewn nests with “...spider silk teased out to make a knot” (page 238); ioras (Aegithina) are “...frequent unknowing hosts to Cacomantis cuckoos” (page 218); Green Broadbills (Calyptomena viridis) show signs of polygyny and maybe even lekking (page 212); nesting barbets make numerous starter holes, possibly “...to deceive snakes which systematically investigate such holes” (page 200). In addition to these taxic introductions, numerous yellow-highlighted paragraphs are interspersed around the book. These convey snippets of natural history that display the Phillipps’ remarkable knowledge of Bornean botany, history, and anthropology. One of these paragraphs describes red bean creepers (Caesalpinias) as a strong attractant for bulbuls, leafbirds, flowerpeckers, and sunbirds. Another relates that spiderhunters (Arachnothera) are divided into two ecological groups, one that feeds in the canopy and the other that “trap-lines” bananas and ginglers. This explains why Little Spiderhunters (A. longirostra) zoom through the understory and—like traplining hermit hummingbirds in the Neotropics (Gill
1988)—are the most commonly mist-netted birds of the Bornean forest. Yet another yellow paragraph describes the traditional native method for snaring pheasants using a “pagar”, or herding fence, and another explains that egrets are the eyes and ears of forest spirits. At the beginning of the Phillipps’ book is an extensive introduction, full of facts on Bornean birds, geography, habitats, weather, etc., virtually everything needed to get started as a birdwatcher or ornithologist in Borneo. I wish I had read this section before traveling to Mt. Pueh in westernmost Sarawak in January 2010. The map and accompanying bar graphs on page 35 indicate that part of Sarawak to be the wettest place in Borneo in January, and I can now vouch that it is true.

The authors are remarkably well suited to produce a natural history guide for Bornean birds. Brother and sister, they grew up in Sabah, spending their childhood exploring such famous sites as Mt. Kinabalu, Sepilok Orangutan Reserve, and the Crocker Range, not to mention many lesser known places. As a boy, Quentin Phillipps wrote a series of papers on the occurrence and nesting of birds (e.g., Phillipps 1970, Phillipps and Phillipps 1970), and has contributed to Bornean ornithology ever since (e.g., Phillipps 1982). The Phillipps family is well known in Sabah for their knowledge of botany and ecology (e.g., Phillipps 1985), and Karen Phillipps is famous for her illustrations in ground-breaking Asian field guides (Viney and Phillipps 1977; Payne et al. 1985; MacKinnon and Phillipps 1993, 2000). Quentin Phillipps’ long-term fascination with birds, Karen Phillipps’ artistic skills, and their combined experiences as Bornean explorers and naturalists come together in this wonderful book, which I could not recommend more highly.—

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LITERATURE CITED


BIRDS OF AUSTRALIA. Eighth Edition. By Ken Simpson and Nicolas Day. Princeton Field Guides, Princeton, New Jersey, USA. 2010: 381 pages and 132 color plates. ISBN: 978-0-691-14692-8. $39.50 (flexible waterproof cover).—This book is a substantial revision of the authors’ earlier editions, a series that has become a standard field guide for Australian birds with over 600,000 copies in print. A table of contents (or “Key”) gives a quick description of each family, color figures of representative birds, and the pages where the families are illustrated in the color plates. The 132 color plates include the common name of each species, and the facing “Field information” page has the common and scientific names, a concise description of the species as it appears in the field, notes on different ages and plumage morphs (especially in raptors), an index of status (resident, migratory nomadic, partially resident), abundance, size, voice, and habitat, and a distribution map (including distinctive races or subspecies); for some species it has alternative and prior names and comments on species relationships where these were only recently discovered. A “Vagrant bird bulletin” after the main color plates is a section for 85 uncommon species and rarities, especially sea-
birds and shorebirds, which have been accepted by the Australian rare birds records committee. This section includes, on a single page for each set of species, the color figures, descriptions, and maps with smaller figures than in the main color plates. End plates sketch the bill profile and plates for the larger petrels, shearwaters, and albatross, life size and with a length calibration; the sketches are useful for identification of beach-washed birds. The biological information and the common and scientific names are consistent with the regional standard on Australian birds (HANZAB 1990–2006), and the family names are those of Christidis and Bowles (2008). The information summarizes a wealth of other recent publications as well. The Birds of Australia is not only a field guide (it is mainly a field guide, pages 18–302); it is also a concise handbook of all the 780 species.

The color plates are the best I have seen of Australian birds, colorful and clear, and generally true to the shape, plumage color, and details of the birds. Perhaps most amazing are the diverse and colorful Australian parrots and the cuckoos. The color plates show the variation in age, male and female, appearance in flight and perched, plumage morphs, and distinctive races. However, the head patterns of the three jaegers (Stercorarius) are not shown as distinctive as they are in the field (adults have a black helmet in Pomarine Jaeger [S. pomarinus], a cap to just below the eye in Parasitic Jaeger [S. parasiticus], and a smaller cap in Long-tailed Jaeger [S. longicaudus]). The male western Splendid Fairywren (Malurus splendidus splendidus) is too purplish; the plumage in Western Australia is bright blue not purple. The “yellow-faced morph” of Gouldian Finch (Erythrura gouldiae) is only slightly less red (to me, “dark orange” or “orange”) than the red-faced morph; nevertheless this plumage has long been known as the “yellow-faced morph”. The birds on a plate are shown on the same scale with additional views of birds in flight and in the distance illustrated at smaller scales. The illustrations are lifelike; all show the identifying features. Some birds are illustrated on a plain background and other birds are shown with a view of their natural habitat. The number of birds on a plate varies according to the species. For examples, the plate for two species of Diomedea albatross has 16 color figures and the facing descriptive page has 15 additional black and white figures of birds seen in flight from below and on the water from the front; the plate for five species of kites shows 25 birds; and the plate for eight species of bulbuls, thrushes, and starlings has 14 birds and a footnote refers to six additional species that are illustrated and described elsewhere in the “Vagrant bird bulletin.” The “Field information” pages are short on bird descriptions; they point out the unique features for identification of the species, and the color figures of the birds largely speak for themselves. There are more than 900 black and white illustrations of chicks, differences between males and females (as in the black cockatoo [Calyptorhynchus] species by bill shape, color and facial pattern), geographic races, face patterns, wing patterns, undertail patterns, tails of snipe (Gallinago) and gerygone (Gerygone) species, and relative size of similar species (one page shows 17 “black bush birds” of Australia), and typical behaviors. The distribution maps show the areas of breeding, nonbreeding, and irregular or nomadic occurrence.

End sections describe and illustrate the habitats in Australia; breeding information about each family including nest site and structure, eggs, parental care (role of male and female, duration of parental care), and breeding season of each species; checklists of Australian island territories; and appendices of hints for birding, an extensive glossary, lists of Australian naturalist organizations and bird books, and indices of Latin names and common names.

The book is a complete and attractive field guide and also a concise source of information on the biology of Australian birds. It is nearly 25 mm (1 inch) taller and wider than the National Geographic Field Guide to the Birds of North America. I recommend the book to everyone with an interest in the birds of Australia.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48104, USA; e-mail: rbpayne@umich.edu

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COVER: Wilson’s Storm Petrel (Oceanites oceanicus). Illustration by Don Radovich.

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Kirtland’s Warblers (Dendroica kirtlandii) are habitat specialists, typically breeding in young jack pine (Pinus banksiana) stands. The species was only known to nest in Michigan, USA, but recently Kirtland’s Warblers were found nesting in a red pine (Pinus resinosa) plantation in central Wisconsin, USA. Photograph of adult male singing from red pine in Adams County, Wisconsin by Joel A. Trick, U.S. Fish and Wildlife Service.
CHARACTERISTICS OF A RED PINE PLANTATION OCCUPIED BY KIRTLAND'S WARBLERS IN WISCONSIN

NICHOLAS M. ANICH,1,2,7 JOEL A. TRICK,3 KIM M. GRVELES,4 AND JENNIFER L. GOYETTE5,6

ABSTRACT.—We studied a newly established population of Kirtland's Warbler (Dendroica kirtlandii) in Adams County, Wisconsin, nesting in a red pine (Pinus resinosa) plantation. We found eight males and five females in Adams County in 2008 and 10 males and 10 females in 2009. Five of seven (71%) males color-banded in 2008 returned in 2009, and at least eight successful nests produced an estimated 33 young over the 2 years. Red pine comprised 66.9% of trees on the main site, 20.6% were northern pin oak/black oak (Quercus eliipsoidalis/Q. velutina), and 12.5% were jack pine (Pinus banksiana). Total tree density at the main site was 1.876 trees/ha, lower than generally reported in Michigan. Percent canopy cover and ground cover types were similar to Michigan sites. Lowest live branch height of jack pine at our site was closer to the forest floor. Significant red pine die-off at our site combined with substantial natural jack pine recruitment created a landscape matrix of openings and thickets that produced suitable Kirtland's Warbler habitat. We suggest young red pine-dominated plantations should be searched when surveying for Kirtland's Warblers as some lower-density red pine plantations could provide important supplemental habitat as the species expands its range.

Kirtland's Warbler (Dendroica kirtlandii) is a habitat specialist that typically breeds in young jack pine (Pinus banksiana) on sandy soils. It is a ground-nester that often exhibits breeding site fidelity and has a tendency to settle in aggregations rather than disperse widely throughout suitable habitat (Mayfield 1960). The only known breeding locality until 1995 was in several counties in the northern Lower Peninsula of Michigan (Mayfield 1992). This species is federally endangered because of its small population size, limited range, and persistent threats. Decennial censuses showed a 60% decline between 1961 and 1971, likely due to Brown-headed Cowbird (Molothrus ater) parasitism and dwindling suitable habitat (Mayfield 1972). Forest management and cowbird removal at the primary breeding site in Michigan helped reverse the population decline, and small numbers of Kirtland's Warblers have nested in the Upper

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Peninsula of Michigan since 1995 (Probst et al. 2003) and in Ontario, Canada since 2007 (Richard 2008).

Occasional observations of Kirtland’s Warblers have been reported in Wisconsin. Early observations were of single birds during migration (e.g., Taylor 1917), and there were only nine confirmed observations prior to 1978 (Tilghman 1979). Singing males were occasionally found in young jack pines in Wisconsin beginning in 1978 during the breeding season. Statewide surveys of jack pine stands on sandy soils in 1978 and 1988 turned up two and eight singing males, respectively (Tilghman 1979, Hoffman and Abernathy 1988). Three singing males were discovered in a red pine (Pinus resinosa) plantation in Adams County, Wisconsin in May 2007. Subsequent intensive searches in 2007 revealed at least eight males, three females, and three nests at that site, but without evidence of fledging (Trick et al. 2008).

Typically sites are only occupied by Kirtland’s Warbler when trees are young (1.5–5 m in height; Mayfield 1992). Pines in these stands generally retain green needles on branches low to the ground (Mayfield 1960, Probst and Weinrich 1993). Occupied stands are also typically characterized by both dense pine thickets and open grassy areas.

Kirtland’s Warbler habitat was historically generated and maintained primarily by wildfires, but forest fragmentation and fire suppression drastically reduced the extent of this habitat type (Mayfield 1992). Currently, the majority of Kirtland’s Warblers breed in jack pine plantations created specifically for the species with the pines planted in opposing sine-wave patterns that alternately create thickets and openings (Donner et al. 2008). Nesting has been infrequently reported in red pine plantations (Mayfield 1960, Anderson and Storer 1976, Walkinshaw 1983, Probst and Weinrich 1993), but with few details. Occupancy of red pine-dominated areas has been considered rare (Huber et al. 2001).

We began monitoring the pioneering population of Kirtland’s Warblers in Wisconsin once the first individual was documented there. The objectives of this paper are to: (1) document site occupancy and nesting success in the first 2 years of colonization, and (2) evaluate the quality of the habitat patches used by the warblers by measuring vegetative parameters at the site. This information will be helpful for future conservation efforts for this endangered species.

METHODS

Study Area.—We studied Kirtland’s Warblers in Adams County, Wisconsin, in commercially-owned red pine plantations. Jack pine and northern pin oak/black oak (Quercus ellipsoidalis/Q. velutina: hereafter “oak”) were common at the sites, while black cherry (Prunus serotina) and bur oak (Q. macrocarpa) were uncommon. Stands consisted of rows in which red pines were generally spaced ~2 m apart and featured irregular grassy openings where pines failed to survive. Ground cover consisted of sedge (Carex pensylvanica), grasses (Andropogon spp. and Panicum sp.), blueberry (Vaccinium angustifolium), forbs, pine needles, mosses and lichens, and downed wood from past timber harvest. Soils of occupied stands were sandy, and conditions in neighboring stands ranged from recently clear-cut to 20-m-tall trees.

Site Occupancy.—We surveyed sites in Adams County, Wisconsin known to have been occupied by Kirtland’s Warblers in previous years from mid-May to mid-July 2008 and 2009. We walked areas of suitable habitat listening and looking for Kirtland’s Warblers, starting about dawn and ending in late morning when singing subsided or the wind increased. We also used song playbacks to search apparently suitable stands within 16 km of previously occupied sites. We used mist nets and song playbacks to target-net, capture, and color-band males (Refsnider et al. 2009, Trick et al. 2009); spot-mapping (Bibby et al. 2000) was used to estimate the extent of males’ territories.

Nest Monitoring.—We followed males to locate females and followed both males and females to locate nests. We systematically searched to locate nests, but this was generally less effective than following birds and detecting cues from the birds. We minimized approaches to nests and generally monitored nests from a distance (4–14 m) to ascertain nest stage and verify they were active. We visited nests at estimated fledging dates to record success (fledged young). We assumed that all young present the last time we looked in the nest had fledged.

Habitat Characteristics.—We collected data from 10 to 12 August 2009 at the stand in Adams County, Wisconsin that had most birds (6 males, 7 females, and 8 nests in 2009). We sampled 40 vegetation points spaced 30 m apart on three evenly-spaced transects in the core area of the stand used by Kirtland’s Warblers, spanning the
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territories of six males. We obtained data that best represented the general nesting habitat at the site by placing transects in the occupied cluster. Transects were east-west to avoid sampling artifacts from north-south planted rows of red pine. Transects averaged 375 m in length and were 100 m apart with 11–15 points per transect. We used point-quarter sampling (Cottam and Curtis 1956) and measured the distance to and species of the nearest tree in each quadrant surrounding each point, allowing us to calculate tree density and relative frequency. We also measured tree height and height of the lowest green branch. We only measured trees that were ≥2.5 cm in diameter at 10 cm from the ground. We also quantified ground cover below 50 cm in a 1-m² quadrat centered at the point. Cover types were classified as blueberry, grasses/sedges, live woody stems, moss/lichens, bare ground, dead woody debris, forbs, pine needles, or leaf litter. We recorded grass and sedge cover separately for 26 of the 40 plots. We used tape measures across 548 m of our transects and quantified the distance (to the nearest 0.03 m) comprised by open area or canopy cover of the three major tree species.

Data Analysis.—We used descriptive statistics to summarize the data. We report number of birds detected and calculate return rate of color-banded males. We report the number of nests, number successful, and estimated number of young fledged. We summarized the data for the stand vegetation measurements using means and 95% confidence intervals (CI). We used the 95% CI to compare stand tree heights and lowest live branch heights to previously published results from Michigan Kirtland’s Warbler breeding areas, specifically wildfire-regeneration areas and plantations (Probst and Weinrich 1993, Bocetti 1994).

RESULTS

Occupancy and Nest Success.—Red pine stands occupied by Kirtland’s Warblers in Adams County in 2008 and 2009 ranged in age from 11 to 13 years (since 2-year-old seedlings were planted) and ranged in size from 36 to 70 ha (T. A. Watson, pers. comm.). Eight male and five female Kirtland’s Warblers were detected in 2008. Five of seven males (71%) color-banded in 2008 returned to the site in 2009. Ten male and 10 female Kirtland’s Warblers were found in 2009. We located five nests in 2008, two of which fledged five Kirtland’s Warbler young each. We found 10 nests in 2009, of which at least six successfully fledged an estimated 23 warbler young. Three of four stands used by Kirtland’s Warbler between 2007 and 2009 were within 3 km. We also detected a single pair in 2009 that successfully nested in a fourth stand, 10 km from the main stands.

Habitat Characteristics.—Total density of trees was 1,876/ha of which 66.9% were red pine (1,254/ha), 20.6% were oak (387/ha), and 12.5% were jack pine (234/ha). Mean tree height was 3.2 m (Fig. 1). Jack pines in the Wisconsin stand were taller than in the Michigan stands, while heights of red pines were similar (Fig. 1). Most oaks at our site were small (mean height = 2.2 m, 95% CI = [1.9, 2.4], n = 33). The height of the lowest live branches of jack pine on the Wisconsin site was similar to heights reported in Michigan (Fig. 2). The lowest live branch of red pine in the Wisconsin stand was closer to the forest floor than for jack pine (Fig. 2). The canopy in the Wisconsin stand was over half open (54%) with red pine dominating the tree canopy (31% cover) followed by oak (9%) and jack pine (6%). Ground cover in the stand was dominated by sedges followed by pine needles and dead woody debris (Fig. 3). We recorded relatively few blueberries, forbs, and grasses. Big bluestem (Andropogon gerardii) was the most common grass in our plots. The most common forb recorded was flowering spurge (Euphorbia corollata), which was present in 15 of 40 plots (38%). Long-branch frostweed (Helianthemum canadense), common sheep sorrel (Rumex acetosella), and starry false Solomon’s seal (Maianthemum stellatum) were each present in four plots.

DISCUSSION

Red pine is not a common breeding habitat for Kirtland’s Warblers, but the persistent occupancy, comparable return rates to that found for birds in jack pine stands, and good nest success demonstrated the suitability of red pine-dominated stands for breeding Kirtland’s Warblers. All four stands in Adams County selected for use by Kirtland’s Warblers were red pine plantations.

The return rate for our small sample of adult males is comparable to reported rates from Michigan of 53–75% (Berger and Radabaugh 1968; Mayfield 1960, 1983; Probst 1986) suggesting males survive and perceive the Adams County site as suitable habitat. Hoover (2003) suggested site fidelity is associated with site quality because birds that breed successfully are
FIG. 1. Heights of trees in stands used by Kirtland's Warblers. White bars are means of all trees from previous studies in Michigan; Probst and Weinrich (P & W 1993) measured 10 wildfire sites, five unburned natural-regeneration sites, three jack pine plantations, and three plantations dominated by red pine; Bocetti (1994) measured 11 wildfire sites and 10 (jack pine) plantation sites. Gray bars are from 160 trees measured at a used site in Adams County, Wisconsin, and include 107 red pine, 33 northern pin oak/black oak, and 21 jack pine. Error bars are 95% confidence intervals.

more likely to return. Breeding has been successful with the cowbird trapping that occurred at our site, and this population appears to be increasing. However, the long-term population dynamics in this habitat type are unknown.

We recognize the limitations of results based on one stand containing the territories of six males, but our data provide important additional information on the full range of habitats successfully used by Kirtland's Warblers (see also Probst and Weinrich 1993). Jack pine is thought to be a requirement for Kirtland's Warbler and natural recruitment of jack pine occurred on all occupied stands in Adams County. The density and percentage of jack pine on our Kirtland's Warbler stand, to our knowledge, is the lowest reported in the literature. J. R. Probst (pers. comm.) observed that 2–3 red pine sites used in Lower Michigan were larger, and had fewer jack pines, than our site. Mayfield (1960:16) reported birds nesting in 1951 in "red-pine plantations where there were few if any jack pines", but did not elaborate further.

Our measurements of pine density and total tree density are low compared to sites used for breeding in Michigan, although plantation sites typically have fewer trees than wildfire sites (Probst 1988, Probst and Weinrich 1993). Stands with fewer than 2,500 trees/ha have been considered marginal Kirtland's Warbler habitat (Probst and Hayes 1987). Houseman and Anderson (2002) found tree densities greater than ours in plantations (2,890 jack pines/ha and 3,345 total trees/ha), and on burned sites at Mack Lake (8,578 jack pines/ha and 8,950 total trees/ha). Bocetti (1994) found an average of 7,000 jack pines/ha on wildfire sites; her measurement of 2,000 jack pines/ha on plantation sites was comparable to our total tree density. However, tree densities alone do not adequately define habitat suitability, because variable tree-spacing can greatly affect canopy cover in a stand, and the wider spacing of trees at
FIG. 2. Height of the lowest live branch on trees in stands used by Kirtland’s Warblers. White bars are means of all trees at 11 wildfire sites and 10 (jack pine) plantation sites in Michigan measured by Bocetti (1994). Gray bars are from 160 trees measured at a used site in Adams County, Wisconsin, and include 107 red pine, 33 northern pin oak/black oak, and 21 jack pine. Error bars are 95% confidence intervals.

plantation sites provides more cover with fewer trees than in naturally regenerated sites (Probst 1988).

Tree height can provide some measure of the stage of a Kirtland’s Warbler stand (Probst and Weinrich 1993). Our population was not monitored before 2007; we do not know how long birds were present at the site and whether our site is just becoming occupied, is in its prime, or is declining. Average heights of jack pines in our study have been typically associated with declining stands (Probst and Weinrich 1993) but red pine-dominated stands may have a different succession scenario. The stand in our study, based on tree canopy cover which increases with stand age, may be in its prime condition for nesting warblers (Probst and Weinrich 1993).

The persistence of low live branches in our stand supports the view that low branch density is an important characteristic of suitable Kirtland’s Warbler habitat; several authors (Mayfield 1960, Probst 1988, Probst and Weinrich 1993) have suggested low live branches are critical for nesting, female foraging, and nestling cover. We frequently observed females and recently fledged young using low branches for foraging and cover, and we found four nests directly beneath very low live red pine branches. The extremely low mean live green branch height shown by red pine at our site may indicate one reason for the settlement of our site by Kirtland’s Warblers. A red pine component to a stand might prolong use of that stand by Kirtland’s Warblers if loss of live green branches is a main reason for abandonment of a stand (Probst 1988).

Ground cover types at our site were comparable to other sites, although our site was more dominated by sedges than most Kirtland’s Warbler sites (Bocetti 1994, Houseman and Anderson 2002, Probst and Donnerwright 2003). Some plants commonly observed in Michigan were not common at our site: bearberry (Arctostaphylos uva-ursi) and sand cherry (Prunus pumila) were present but not common, and we observed no sweet fern (Comptonia peregrina). The dominance of sedges and relative lack of forbs and grasses at our site may be related to application of herbicide during site preparation, although others
FIG. 3. Ground cover measurements in 1-m$^2$ plots in a stand used by Kirtland’s Warblers in Adams County, Wisconsin in 2009. Error bars are 95% confidence intervals. Means are from 40 plots, except for grasses and sedges, which are from 26 plots we separately recorded for those two cover types. The mean of grasses + sedges was recorded for all 40 plots, and was 46.1% (95% CI = 35.7, 56.4).

have reported the tendency of Carex pensylvanica to form dense mats in jack pine stands following disturbance, which may inhibit growth of blueberry and jack pine (Abrams and Dickmann 1982, Houseman and Anderson 2002, Probst and Donnerwright 2003). Probst and Donnerwright (2003) noted that ground cover does not seem to be a limiting factor for Kirtland’s Warbler nest sites or habitat suitability, as a wide range of ground cover types occurs on appropriate sites.

CONSERVATION IMPLICATIONS

The extensive die-off of planted red pine and substantial natural jack pine recruitment at the Adams County site provided a landscape matrix of openings and thickets that produced suitable Kirtland’s Warbler habitat. We believe that, except for these circumstances, this stand would not be suitable for occupation by Kirtland’s Warblers, and that most planted red pine plantations do not create the habitat conditions required by the species. Future management mimicking the conditions at our site, featuring thickets of jack pine complementing reduced numbers of red pine interspersed with openings (see Probst 1988), could prove fruitful. The inclusion of more-profitable red pine in this configuration might provide an incentive for timber companies to plant some stands in configurations that support Kirtland’s Warblers, resulting in supplemental habitat beyond traditional jack pine stands.

Understanding the characteristics of future occupied stands throughout the area of range expansion is essential if the total Kirtland’s Warbler population continues to increase. The potential suitability of red pine-dominated sites could become increasingly important if jack pine continues to be converted to red pine. More study is needed on the characteristics that affect suitability of red pine-dominated stands for Kirtland’s Warblers, especially how suitability of these sites changes over time.

ACKNOWLEDGMENTS

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LITERATURE CITED


AVIAN COMMUNITY AND MICROHABITAT ASSOCIATIONS OF CERULEAN WARBLERS IN ALABAMA

JOHN P. CARPENTER, YONG WANG, CALLIE SCHWEITZER, AND PAUL B. HAMEL

ABSTRACT.—Cerulean Warblers (Dendroica cerulea) have experienced one of the highest population declines of any neotropical–Nearctic migratory species in North America. We performed point counts and habitat assessments in areas used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons to examine their avian associations and identify microhabitat features that best explained their occurrence. We detected on average ~50 Cerulean Warbler males (total) in three disjunct populations during each breeding season. Areas used by Cerulean Warblers were characterized by avian communities with significantly higher species richness, diversity, and abundance compared to areas where they were not detected. Correspondence analysis related Cerulean Warblers to inhabitants of riparian, bottomland deciduous forests (e.g., Kentucky Warbler [Oporornis formosus], Acadian Flycatcher [Empidonax virescens], and Northern Parula [Parula americana]) and two edge specialists (Blue-winged Warbler [Vermivora cyanoptera] and Indigo Bunting [Passerina cyanea]) suggesting Cerulean Warblers in our study areas may be tolerant of some habitat disturbance within an otherwise largely forested landscape. Information theoretic criteria and canonical correspondence analysis indicated Cerulean Warblers preferred bottomland forests containing tall (> 29 m), large diameter, well-spaced (> 27 m/ha) deciduous trees with greater canopy cover (~90%), closer (< 20 m) canopy gaps, fewer snags (~25/ha), and a moderately complex canopy structure.

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The Cerulean Warbler (Dendroica cerulea) has lost nearly 70% of its breeding population since 1966 (Rich et al. 2004) because of alterations in breeding, migratory, and wintering habitats compounded by the bird’s dependence on extensive tracts of large deciduous trees in many parts of its range (Hamel 2000a). Northern Alabama historically represented a portion of the Cerulean Warbler’s southern-most breeding range where they were described as common and even numerous in several counties throughout the state (Imhof 1976). This warbler is now rarely encountered in Alabama during the breeding season and was designated a Priority One species (highest conservation concern) by the Alabama Department of Conservation and Natural Resources (Mirarchi et al. 2004).

Selection of breeding territories by landbirds is heavily influenced by structure and composition of the surrounding habitat and avian community (MacArthur and MacArthur 1961, Wiens 1989). Thus, effectiveness of management initiatives is dependent upon not only identifying the habitat requirements of the species under investigation, but also the avian community with which it associates. Recent studies of Cerulean Warblers emphasize breeding habitat requirements (Robbins et al. 1992, Jones and Robertson 2001, Weakland and Wood 2005, Barg et al. 2006b), nesting behavior (Oliarnyk and Robertson 1996, Barg et al. 2006a, Rogers 2006, Roth and Islam 2008), and habitat management (Hamel 2005, Hamel et al. 2005b, Hamel and Rosenberg 2007), while information regarding avian associations of Cerulean Warblers remains scarce (Jones et al. 2004) and anecdotal (Lynch 1981, Hamel 2006).

Recent discoveries of two small Cerulean Warbler populations in Alabama suggest habitat is available in this portion of the species range to support small breeding populations (Carpenter et al. 2005). This study was initiated in response to the Rosenberg et al. (2000) recommendation for additional Cerulean Warbler research in Alabama to provide more accurate population estimates and habitat requirements needed to effectively manage habitat for this species. Our objectives were to: (1) examine avian associations of the Cerulean Warbler to facilitate a better understanding of this species' habitat use and the bird community in which it breeds, and (2) identify microhabitat features that best explain Cerulean Warbler occurrence in the southern portion of its range where populations are in serious decline (Buehler et al. 2008).
METHODS

Study Areas.—We studied Cerulean Warblers at three sites in northern Alabama during the 2005 and 2006 breeding seasons (Fig. 1). The most recently discovered Cerulean Warbler populations are in Jackson County along Hurricane Creek in the Walls of Jericho tract of Skyline Wildlife Management Area (WMA) (34° 58' N, 86° 6' W) and on private property along Larkin Fork (34° 57' N, 86° 13' W). Both Jackson County populations breed in bottomland hardwood forest of the Mid-Cumberland Plateau where vegetation is dominated by mature (80+ year-old) forest categorized as oak and oak-hickory (Quercus spp.-Carya spp.) with mixed mesophytic communities restricted to valleys and coves (Braun 1950). Additional canopy species include box elder (Acer negundo), elm (Ulmus spp.), hackberry (Celtis occidentalis), tulip poplar (Liriodendron tulipifera), sugar maple (Acer saccharum), American beech (Fagus grandifolia), eastern sycamore (Platanus occidentalis), and black walnut (Juglans nigra). Several maintained fields averaging...
2 ha in size occur throughout the floodplains of these sites. A third Cerulean population is in Lawrence County within the 71,600-ha Bankhead National Forest (34°20' N, 87°22' W). Bankhead National Forest (BNF) is along the southern Cumberland Plateau and is characterized by dissected sloping ridges and rock bluffs dominated by lobolly pine (Pinus taeda), upland hardwood, and mixed hardwood-pine with additional canopy species similar to those at the Jackson County sites (USDA Forest Service 2004). Cerulean Warblers are concentrated in BNF along the floodplain forests of the 4,200-ha Sipsey Wilderness Area.

**Bird Surveys.**—We surveyed Cerulean Warblers from May to June during the breeding seasons of 2005 and 2006 by walking the floodplains and adjacent slopes of Hurricane Creek and Larkin Fork, and along Flanigan and Borden creeks in Bankhead National Forest. We mapped male Cerulean territories on multiple visits using radiotelemetry, repeated observations of color-banded males, and by distinguishing song variability between neighbors (Woodward 1997). Ten-minute, fixed-radius point counts \( n = 53 \) were performed within a territory and centered under individual, singing male Cerulean Warblers. All counts were conducted once at each location prior to 1030 hrs EST following Hamel et al. (1996) by a single observer to eliminate multiple surveyor bias (Sauer et al. 1994).

Point counts were also performed once at 47 additional locations from May to June 2005 and 2006 in an effort to locate new breeding populations (Fig. 1). We concentrated our sampling effort in Skyline WMA and Bankhead NF to reduce spatial variability; however, our only requirements for these locations were that they must occur in deciduous/mixed forest and the Cerulean Warbler's historic breeding range in Alabama (Imhof 1976). We used the ArcGIS (Version 9.1, ESRI 2005) extension Hawth's Tools (Beyer 2004) to generate 26 random points: 12 in Skyline WMA, six in Bankhead NF, and eight in state parks and nature preserves. An additional 19 locations were selected from 122 pre-existing point count stations in Bankhead NF (USDA Forest Service 1995). The remaining two locations were based on Cerulean Warbler observations from Alabama Breeding Bird Atlas surveys in 1999 and 2001 (R. L. West, pers. comm.) in an effort to verify the continued existence of breeding Cerulean Warblers. Playback of a conspecific song was broadcast for 5 min at the conclusion of these counts to ensure that no Cerulean Warblers were present.

**Microhabitat Characteristics.**—We compared microhabitat from used habitat \( n = 52 \) centered at point counts conducted under Cerulean Warbler males, and in unused habitat \( n = 47 \) defined as point count locations where Cerulean Warblers were not detected. Habitat measurements for one used point count were not collected due to logistic constraints. The median distance between used locations in the year of sampling was 192.9 m (interquartile range = 112.4–383.6) and 2.1 km (interquartile range = 1.0–2.8) between unused locations. Vegetation was measured by one observer within 0.04-ha (11.3-m radius) circular plots following James and Shugart (1970) and Noon (1981). Plot measurements included basal area, total live stems ≥3-cm diameter at breast height (DBH), total snags ≥8-cm DBH, tree height, slope, aspect, understory density, and distance to and size of nearest canopy gap. Percent canopy cover was estimated from 40 ± vertical readings along transects in the cardinal directions using an ocular densitometer tube. Each reading was assigned one of four height intervals (0-5, 5-15, >15-25, >25 m, or no cover) to estimate canopy structure complexity. Slope was measured in degrees using a clinometer and aspect was transformed to a value ranging from 0.0 to 2.0 (Beers et al. 1966). This distinguished less productive, southwest facing slopes (value = 0.0) from more productive, mesic northeast slopes (value = 2.0) (van Manen et al. 2005). We assigned flat plots a neutral value of 1.0. Distance to and size of the nearest canopy gap <50 m from plot center and ≥10 m² were measured following Runkle (1992).

**Analysis of Point Counts.**—All nocturnal, colonial, and raptor species including birds with restricted vocalizations (e.g., hummingbirds), were excluded from the analysis because of the difficulty of reliably detecting them during diurnal point counts (Bibby et al. 2000). Species richness was calculated as the total number of species detected during each count, and total number of individuals counted at each location was used as bird abundance. Species diversity was estimated with the Shannon-Weiner index using the Microsoft® Office Excel (Microsoft Inc. 2003) macro Biological Tools Version 0.2 (Hanks 1995). We constructed a conservation concern value using designations developed by the Alabama Nongame
Wildlife Division (Mirarchi et al. 2004), and summed the number of species designated moderate or higher detected at each count. We pooled data from both seasons to increase sample size because multivariate analysis of variance (MANOVA) tests suggested there was no interaction or the trend was consistent between year and type of survey (used vs. unused) for habitat variables (Philai's Trace = 0.11, $F = 0.51$, df = 18 and 78, $P = 0.95$) and for avian community variables (e.g., abundance, richness and diversity index, Philai's Trace = 0.08, $F = 2.10$, df = 4 and 93, $P = 0.09$). Independent sample $t$-tests were used to test for differences between used and unused plots in bird species richness, abundance, diversity, and conservation concern values, as well as abundance of Brown-headed Cowbirds (Molothrus ater) and three common nest predators: American Crow (Corvus brachyrhynchos), Blue Jay (Cyanocitta cristata), and Red-bellied Woodpecker (Melanerpes carolinus).

**Analysis of Avian Community Associations.**—Detrended correspondence analysis (DCA) was used with bird abundance to help explain the structure of the sampled avian community (Hill and Gauch 1980). We chose nonlinear scaling and detrended the axes using second-order polynomials following Longman et al. (1995) to avoid the limitations inherent in DCA, including distorted gradient structure and a lack of robustness (Minchin 1987). Rare species were down-weighted and ordination scores were obtained with biplot scaling focused on inter-species distances using CANOCO 4.54 (ter Braak and Smilauer 2006). We referenced Birds of North America accounts (Poole 2005) for general habitat preferences of each species to assist in interpretation of DCA axes, and excluded species detected at less than three locations to reduce the effect of transient or accidental species (Wakeley et al. 2007).

**Analysis of Microhabitat Characteristics.**—We attempted to correct any variables with non-normal distributions using Shapiro-Wilk tests and square root or logarithmic transformations. Independent sample $t$-tests were used to compare mean measurements of vegetation from used habitat plots with unused plots, and two-sample Mann-Whitney $U$-tests for variables that violated normality or equal variance assumptions. Canopy structure complexity was estimated with the Shannon-Weiner diversity index expressed as a proportion of the maximum possible diversity using the number of readings assigned to each height interval (Zar 1999).

**Analysis of Microhabitat and Avian Community.**—We used principal components analysis (PCA) to reduce the dimensionality of the original microhabitat variables. All components had variance inflation factors <1.1 and were considered to be unique contributors to the analysis (Leps and Smilauer 2003). Canonical correspondence analysis (CCA) was used to expose patterns of variation in avian community composition and species abundance related to PCA variables (ter Braak 1986), and to guide selection of habitat characteristics for modeling Cerulean Warbler microhabitat. The length of the longest gradient (i.e., ordination axis) was 5.08, and we considered unimodal ordination methods (e.g., CCA) more appropriate than linear methods (e.g., redundancy analysis) (Leps and Smilauer 2003). We used bird abundance and confined the CCA to those species detected at three or more locations within 50 m of plot center using CANOCO 4.54. This is preferable to analyzing all bird detections, which assumes vegetative measures within our plots are an adequate representation of habitats used by birds that were detected farther away where microhabitat characteristics are likely to vary. We used randomized Monte Carlo tests ($n = 499$) to evaluate significance of CCA axes.

**Analysis of Microhabitat and Avian Community Associations.**—We used logistic regression to examine the relationship between Cerulean Warbler occurrence and habitat variables with the binary dependent variable representing used and unused habitat plots. We established 20 models a priori and compared them using the information-theoretic approach of Burnham and Anderson (2004). Variable selection was based on Cerulean Warbler literature (Hamel 2000a), as well as habitat plot comparisons, CCA, and field observations from this study. We performed a second-order bias correction ($\text{AIC}_c$) because $n/K < 40$ and calculated evidence ratios based on Akaike weights ($w_i$) as an indication of model strength in comparison to other models considered (Burnham and Anderson 2004). We examined a variable's beta coefficient to identify its relationship (positive or negative) to Cerulean Warbler presence. Variables present in the model with the highest $w_i$ were considered the best predictors for Cerulean Warbler occurrence.

An alpha level of 0.1 was selected for all tests of significance due to the conservation status of the Cerulean Warbler (Askins et al. 1990). All statistical analyses, unless previously described, were performed using SPSS ® Version 15.0 (SPSS).
RESULTS

Bird Surveys.—Approximately 50 Cerulean Warbler males were detected in northern Alabama during each of the 2005 and 2006 breeding seasons. Cerulean Warblers were found only in Jackson County along Larkin Fork and Hurricane and Mill creeks in Walls of Jericho, and Lawrence County in Bankhead National Forest along Borden, Flannigan, and Horse creeks. No Cerulean Warblers were encountered at unused points or during additional target searches throughout Jackson County or BNF. Walls of Jericho had the highest number of detections with 20 males followed by 15 territorial males in Bankhead National Forest.

Bird species richness ($t = 4.91$, df = 98, $P < 0.01$), abundance ($t = 3.85$, df = 98, $P < 0.01$), diversity ($t = 4.99$, df = 98, $P < 0.01$), and conservation concern values ($t = 9.06$, df = 98, $P < 0.01$) were significantly higher in areas where Cerulean Warblers were detected compared to areas where they were not found (Fig. 2). We detected no difference in abundance of Brown-headed Cowbird ($t = 1.06$, df = 98, $P < 0.29$), American Crow ($t = -0.63$, df = 98, $P < 0.52$), Blue Jay ($t = -1.01$, df = 98, $P < 0.31$), or Red-bellied Woodpecker ($t = 0.85$, df = 98, $P < 0.40$) between used and unused locations.

Avian Community Associations.—The proportion of variance explained by the DCA ordination was 23.7% with the first two axes accounting for greater than half of the variability (13.5%). Species most closely associated with Cerulean Warblers were Kentucky Warbler (Oporomis formosus), Northern Parula (Parula americana), Acadian Flycatcher (Empidonax virescens), Blue-winged Warbler (Vermivora cyanoptera), Louisiana Waterthrush (Parkesia motacilla), American Redstart (Setophaga ruticilla), Belted Kingfisher (Megaceryle alcyon), and Indigo Bunting (Passerina cyanea) (Fig. 3). Bird community associations revealed by the DCA suggested Axis 1 represented a gradient from xeric upland to mesic bottomlands, while Axis 2 distinguished interior deciduous forest from edge and mixed forest habitat.

Microhabitat Characteristics.—Used plots, when compared to unused habitat, had significantly fewer live trees ≥3 cm DBH ($t = -4.01$, df = 97, $P < 0.01$, Table 1), higher ratio of basal area to number of stems ($t = 3.56$, df = 97, $P < 0.01$), greater percentage of deciduous basal area ($Z = -4.5$, df = 97, $P < 0.01$), taller lower,
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FIG. 3. Plot based on detrended correspondence analysis of bird abundance from locations used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. Axis gradients represent general habitat preferences (Poole 2005). ACPI. (Acadian Flycatcher), AMCR (American Crow), AMRE (American Redstart), BEKJ (Belted Kingfisher), BGGN (Blue-gray Gnatcatcher, Polioptila caerulea), BHCO (Brown-headed Cowbird), BLJA (Blue Jay), BTNW (Black-throated Green Warbler, Dendroica virens), BWWA (Blue-winged Warbler), CACH (Carolina Chickadee, Poecile carolinensis), CERW (Cerulean Warbler), COYE (Common Yellowthroat, Geothlypis trichas), DOWO (Downy Woodpecker, Picoides pubescens), EAPH (Eastern Phoebe, Sayornis phoebe), EATO (Eastern Towhee, Pipilo erythrophthalmus), EAWP (Eastern Wood-Pewee, Contopus virens), ETTI (Tufted Titmouse, Baeolophus bicolor), GCFL (Great Crested Flycatcher, Myiarchus crinitus), HAWO (Hairy Woodpecker, Picoides villosus), HOWA (Hooded Warbler, Wilsonia citrina), INBU (Indigo Bunting), KEWA (Kentucky Warbler), LOWA (Louisiana Waterthrush), NOBO (Northern Bobwhite, Colinus virginianus), NOCA (Northern Cardinal, Cardinalis cardinalis), NOPA (Northern Parula), OVEN (Ovenbird, Seiurus aurocapilla), PIWA (Pine Warbler, Dendroica pinus), PIWO (Pileated Woodpecker, Dryocopus pileatus), PRAW (Prairie Warbler, Dendroica discolor), RBWO (Red-bellied Woodpecker), REVl (Red-eyed Vireo, Vireo olivaceus), SUTA (Summer Tanager, P. rubra), WBNU (White-breasted Nuthatch, Sitta carolinensis), WEVI (White-eyed Vireo, Vireo griseus), WEWA (Worm-eating Warbler, Helminthophanes virens), WOTH (Wood Thrush, Hylocichla mustelina), YBCU (Yellow-billed Cuckoo, Coccyzus americanus), YTVI (Yellow-throated Vireo, Vireo flavifrons), YTWA (Yellow-throated Warbler, Dendroica dominica).

We extracted six components from the PCA, which accounted for 67.4% of the cumulative variance (Table 2). Canonical correspondence analysis produced four significant axes (F = 1.46, P < 0.01) that explained 83.8% of the total variance with the first two axes accounting for greater than half of the variability (53.9%). Cerulean Warblers displayed the strongest relationships with the principal component representing high percent deciduous basal area, fewer trees...
TABLE 1. Microhabitat characteristic comparisons for Cerulean Warbler study plots in northern Alabama during the 2005 and 2006 breeding seasons. Values are means (± SE) for t-tests and median (interquartile range) for Mann-Whitney U-tests of untransformed variables. Bold type denotes significant differences, *P* < 0.1.

<table>
<thead>
<tr>
<th>Variable code</th>
<th>Variable description</th>
<th>Used (n = 52)</th>
<th>Unused (n = 47)</th>
<th>df</th>
<th>dfl</th>
<th>dfr</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>Basal area of live trees (m²/ha)</td>
<td>27.8 ± 1.5</td>
<td>25.6 ± 1.2</td>
<td>97</td>
<td>1.13</td>
<td>0.25</td>
<td>0.01</td>
</tr>
<tr>
<td>NTREE*</td>
<td>Number of live trees (ha)</td>
<td>840.4 ± 45.6</td>
<td>1,305.3 ± 121.1</td>
<td>97</td>
<td>-4.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>RBATR</td>
<td>BA:NTREE</td>
<td>0.04 ± 0.003</td>
<td>0.03 ± 0.003</td>
<td>97</td>
<td>3.56</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>SNAG</td>
<td>Number of snags (ha)</td>
<td>25.0 (25.0–68.8)</td>
<td>50.0 (25.0–100.0)</td>
<td>97</td>
<td>-1.51</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>SNAGBA</td>
<td>Basal area of snags (m²/ha)</td>
<td>0.6 (0.1–1.9)</td>
<td>1.0 (0.3–2.4)</td>
<td>97</td>
<td>-1.12</td>
<td>0.26</td>
<td>0.26</td>
</tr>
<tr>
<td>RBASNAG</td>
<td>SNAGBA:SNAG</td>
<td>0.01 (0.01–0.03)</td>
<td>0.02 (0.03)</td>
<td>97</td>
<td>-0.51</td>
<td>0.61</td>
<td>0.61</td>
</tr>
<tr>
<td>DECBAT</td>
<td>Deciduous tree BA (%)</td>
<td>100.0 (100.0–100.0)</td>
<td>96.2 (77.8–100.0)</td>
<td>97</td>
<td>-4.50</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>TRDBH</td>
<td>Diameter nearest tree (cm)</td>
<td>22.0 ± 1.6</td>
<td>13.5 ± 1.1</td>
<td>97</td>
<td>5.49</td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>LOWHT</td>
<td>Lower canopy height (m)</td>
<td>5.8 ± 0.2</td>
<td>5.2 ± 0.2</td>
<td>97</td>
<td>1.69</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>MIDHT</td>
<td>Mid canopy height (m)</td>
<td>17.0 ± 0.4</td>
<td>15.5 ± 0.5</td>
<td>97</td>
<td>2.58</td>
<td>0.01</td>
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<tr>
<td>UPHT</td>
<td>Upper canopy height (m)</td>
<td>29.4 (24.9–31.6)</td>
<td>26.4 (22.4–31.2)</td>
<td>97</td>
<td>1.68</td>
<td>0.09</td>
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<tr>
<td>CCVRF</td>
<td>Canopy cover (%)</td>
<td>90.0 (83.1–95.0)</td>
<td>82.5 (77.5–90.0)</td>
<td>97</td>
<td>-3.48</td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>CSTRC</td>
<td>Canopy structure</td>
<td>0.72 ± 0.02</td>
<td>0.75 ± 0.01</td>
<td>97</td>
<td>-1.64</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>GAPDIST</td>
<td>Distance to nearest gap</td>
<td>2.0 (1.0–3.0)</td>
<td>2.0 (1.0–5.0)</td>
<td>97</td>
<td>-0.71</td>
<td>0.48</td>
<td>0.48</td>
</tr>
<tr>
<td>GAPPSz</td>
<td>Size of nearest gap</td>
<td>3.0 (1.0–4.0)</td>
<td>1.0 (1.0–4.0)</td>
<td>97</td>
<td>-1.69</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>UNDSTRY*</td>
<td>Understory density (stems/ha)</td>
<td>77.6 ± 90.4</td>
<td>1.132.4 ± 92.4</td>
<td>97</td>
<td>-3.23</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>SLOPE</td>
<td>Slope (degree)</td>
<td>8.0 (0.0–21.4)</td>
<td>8.5 (0.0–14.0)</td>
<td>97</td>
<td>-0.64</td>
<td>0.52</td>
<td>0.52</td>
</tr>
<tr>
<td>ASPECT</td>
<td>Aspect</td>
<td>1.0 (1.0–1.3)</td>
<td>1.0 (0.9–1.5)</td>
<td>97</td>
<td>-0.19</td>
<td>0.84</td>
<td>0.84</td>
</tr>
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</table>

* Logarithmic or square root transformation.
* Shannon-Wiener diversity index.
* Relative size 1 (< 30), 2 (30–100), 3 (100–400), 4 (400–1,000), 5 (> 1,000 m²).
* Relative size 1 (1–10), 2 (10–30), 3 (30–100), 4 (> 100 m²).
* Transformed *A* = cos⁴5 - A) + 1 (Beers et al. 1986).

TABLE 2. Principal components analysis of microhabitat characteristics from plots used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. Factor loadings < 0.25 not displayed.

<table>
<thead>
<tr>
<th>Original variables</th>
<th>Rotated factor loadings*</th>
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<tr>
<td></td>
<td>PCAI</td>
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<tr>
<td>RBATR</td>
<td>0.88</td>
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<tr>
<td>BA</td>
<td>0.83</td>
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<tr>
<td>TRDBH</td>
<td>0.70</td>
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<tr>
<td>UPHT</td>
<td>0.61</td>
</tr>
<tr>
<td>LOWHT</td>
<td>0.48</td>
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<tr>
<td>MIDHT</td>
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</tr>
<tr>
<td>GAPPSz</td>
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<tr>
<td>GAPDIST</td>
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</tr>
<tr>
<td>SNAGBA</td>
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</tr>
<tr>
<td>RBASNAG</td>
<td></td>
</tr>
<tr>
<td>NSNAG</td>
<td></td>
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<td>DECBAT</td>
<td></td>
</tr>
<tr>
<td>NTREE</td>
<td></td>
</tr>
<tr>
<td>UNDSTRY</td>
<td></td>
</tr>
<tr>
<td>CSTRC</td>
<td></td>
</tr>
<tr>
<td>CCVRF</td>
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<tr>
<td>ASPECT</td>
<td></td>
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<td>SLOPE</td>
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* Rotation method: varimax with Kaiser normalization.

DISCUSSION

The closest associates of Cerulean Warblers were neotropical migratory species that breed near streams (Louisiana Waterthrush and Northern Parula, but also Belted Kingfisher) in moist woodlands and deciduous bottomland forests (Kentucky Warbler, American Redstart, and Acadian Flycatcher). Cerulean Warblers were not related to species that typically favor xeric...
upland, mixed forests, and edge habitats; however, Indigo Buntings and Blue-winged Warblers, two species common in shrub and edge habitats, were closely associated with Cerulean Warblers. These patterns suggest Cerulean Warblers may be tolerant of small-scale disturbances within the otherwise large, contiguous forest tracts in which they are found (Hunter et al. 2001, Jones et al. 2001, Hamel et al. 2005a, Wood et al. 2005).

We observed Northern Parulas and Red-eyed Vireos reacting aggressively to Cerulean Warbler playback and engage in direct physical contact with Cerulean Warbler males on several occasions (JPC, pers. obs.; Jones et al. 2007). Both of these species are common canopy-dwellers in bottomland deciduous forests whose resource selection likely overlaps that of Cerulean Warblers. We detected no difference between counts of common nest predators and Brown-headed Cowbird abundance; however, the latter species was plotted near Cerulean Warblers along one axis of our ordination and may be attracted to the same edge habitat Blue-winged Warblers and Indigo Buntings are using. We did not examine these relationships in detail but acknowledge that more research is needed to learn if abundance and behavior of competing, predatory, and brood parasitic species are limiting productivity of Cerulean Warblers in Alabama.

We found Cerulean Warblers breeding in communities with more individuals and species, higher species diversity, and a greater number of species of conservation concern compared to areas where they were absent. Bird species richness and abundance increase as habitat patches increase in area and heterogeneity (Free-mark and Merriam 1986, Blake and Karr 1987), which is characteristic of the forested landscapes surrounding our Cerulean Warbler populations (Carpenter 2007). Cerulean Warblers were not effective bio-indicators for overall species diversity in Ontario, but were suited as an umbrella species for similar, canopy-dwelling birds (Jones et al. 2004). Our results also suggest managing forests for Cerulean Warbler habitat may create habitat and improve conservation prospects for several additional species.

Many of our results mirror findings from similar studies throughout the Cerulean Warbler’s range and agree with the general assumptions of Cerulean Warbler selection of microhabitat characteristics, including large diameter trees, less dense understory, and taller upper canopy (Lynch 1981, Jones and Robertson 2001, Wood et al. 2006). However, some

<table>
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<th>Model</th>
<th>L</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>ML</th>
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<td>DECBA(+), ASPECT(-), CSTRC(-), GAPDIST(-), RBASNG(-), RBATR(+), TRDBH(+)</td>
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<td>8</td>
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<td>1.00</td>
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<td>112.00</td>
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<td>78.70</td>
<td>7</td>
<td>107.00</td>
<td>6.65</td>
<td>0.04</td>
<td>0.03</td>
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<td>69.47</td>
<td>11</td>
<td>111.00</td>
<td>6.75</td>
<td>0.03</td>
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<td>81.36</td>
<td>7</td>
<td>107.00</td>
<td>9.31</td>
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<tr>
<td>NTREE(-), DECBA(+), GAPPSZ(+), GAPDIST(-), CCVR(+)</td>
<td>85.63</td>
<td>6</td>
<td>106.00</td>
<td>11.32</td>
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<tr>
<td>RBATR(+), BA(+), TRDBH(+), UPHT(-), LOWHT(+), MIDHT(-), DECBA(+), NTREE(-), UNDSTRY(±)</td>
<td>86.48</td>
<td>6</td>
<td>106.00</td>
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<tr>
<td>DECBA(+), NTREE(-), UNDSTRY(±)</td>
<td>92.69</td>
<td>4</td>
<td>104.00</td>
<td>13.97</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

These patterns suggest Cerulean Warblers may be tolerant of small-scale disturbances within the otherwise large, contiguous forest tracts in which they are found (Hunter et al. 2001, Jones et al. 2001, Hamel et al. 2005a, Wood et al. 2005).
Over one-third of our plots (38.5%) were in flat bottomlands, and Cerulean Warblers displayed a strong negative relation to increasing slope and aspect. Cerulean Warblers are cited as inhabiting ridge tops throughout Appalachia, but this trend diminishes toward the peripheries of its distribution (Rosenberg et al. 2000). The apparent preference for floodplain forests in Alabama may be in response to extensive logging practices of the early 20th century in the Cumberland Mountains (Smalley 1984), which typically focused activity along ridge tops and may have forced Cerulean Warblers to lower elevations (Hamel 2000a). However, all three populations were in highly dissected areas, and the surrounding topography may still have an important role in a Cerulean Warbler’s hierarchical process of selecting breeding habitat in Alabama.

Canopy complexity has received considerable attention in Cerulean Warbler habitat studies. Differences were evident as environmental conditions near the edge of a species’ distribution can vary from those within the core of its range (Lawton 1993, Brown et al. 1995).
(Hamel 2000b, Jones and Robertson 2001, Jones et al. 2001, Hamel 2005). Our average Shannon-Weiner index for used plots was 0.72 ± 0.01 (maximum 1.0) and indicates a moderately complex canopy structure. The disparity between our used and unused plots may be due to use of crude interval measurements which did not accurately distinguish finer complexities at a significance level of 0.1. This may also clarify why Cerulean Warbler presence was negatively related to canopy structure in our modeling. A more complex canopy structure at unused plots does not necessarily indicate an abundance of suitable habitat is available elsewhere in Alabama for Cerulean Warblers. The unused plots' lack of other microhabitat characteristics (e.g., high percent deciduous basal area and fewer but well-spaced, large diameter trees) identified as important to Cerulean Warblers will likely prevent these areas from supporting future populations, if current conditions persist.

The importance of canopy gaps to Cerulean Warbler territory and nest site selection has been supported by some studies (Oliarnyk and Robertson 1996, Nicholson 2004) and questioned by others (Jones et al. 2001, Hamel 2005, Barg et al. 2006b). Used plots had significantly larger canopy gaps compared to unused plots, and our top model indicated Cerulean Warbler presence increased as distance to a canopy gap decreased. Cerulean Warblers in our study may be exploiting these openings as supplemental foraging areas throughout the breeding season and during post-breeding dispersal (Blake and Hoppes 1986, Vitz and Rodewald 2006), and to increase vocal deliverance and recognition of neighboring conspecifics (Barg et al. 2006b). Cerulean Warblers may also be using openings <10 m² created by smaller stature, another variable present in our best supported model, which may be contributing to forest heterogeneity and canopy complexity (Oliarnyk and Robertson 1996, Wood et al. 2006; but see Barg et al. 2006b). Our ordination, however, contradicts these findings by disassociating the principal component representing canopy gaps with Cerulean Warblers. A plausible explanation is the cleared fields maintained within the heavily forested landscape of the Jackson County populations possibly influenced comparison with the more fragmented landscape surrounding unused locations (Carpenter 2007). The appropriate size, quantity, and distribution of canopy gaps and other small-scale disturbances, as well as evidence of whether or not Cerulean Warblers are using them, remains unclear in Alabama.

Our results help clarify the roles of avian species assemblages and vegetative characteristics in habitat used by Cerulean Warblers. This dynamic relationship is further complicated by resource availability, predation, competition with other organisms, and habitat alteration; none of which was accounted for in our study. Future Cerulean Warbler research in Alabama and elsewhere will benefit by addressing these issues in more detail.

ACKNOWLEDGMENTS

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COURTSHIP DISPLAYS AND NATURAL HISTORY OF SCINTILLANT 
(SELASPHORUS SCINTILLA) AND VOLCANO 
(S. FLAMMULA) HUMMINGBIRDS

CHRISTOPHER J. CLARK,1,3 TERESA J. FEO,1 AND IGNACIO ESCALANTE2

ABSTRACT.—The natural histories of Volcano (Selasphorus flammula) and Scintillant (S. scintilla) hummingbirds are poorly known. We describe aspects of their breeding behavior with emphasis on courtship displays and sounds that males produced for females. Males of neither species sang undirected song. Males of both species produced a display dive, in which they ascended ~25 m in the air and then dove, swooping over the female. Both species produced a pulsed sound that was synchronized with abrupt tail spreads during the bottom of the dive. The second rectrix (R2) of both species was capable of generating the same sound in a wind tunnel, suggesting these sounds were made by the tail. The dive sounds of the Volcano Hummingbird were louder than those of the Scintillant Hummingbird. Male Scintillant Hummingbirds produced a wing trill in flight, and performed a shuttle display to females in which the wing-beat frequency reached ~100 Hz. Males held territories in open areas during the breeding season. Not all territories included abundant floral resources, and abundant resources in closed habitat were not defended. The role of resources is unclear in the breeding system of these two species. Received 6 May 2010. Accepted 1 December 2010.

The basic natural history of most Central and South American species is poorly known, compared to North American birds. For example, of the seven species in the hummingbird clade Selasphorus, courtship displays consisting of both dives and shuttle displays have been described for Allen’s (S. sasin) (Aldrich 1938. Mitchell 2000), Rufous (S. rufus) (Calder 1993, Hurly et al. 2001), and Broad-tailed (S. platycercus) (Calder and Calder 1992) hummingbirds, as well as Calliope Hummingbird (Stellula calliope) (Tamm et al. 1989, Calder and Calder 1994), which is phylogenetically nested within Selasphorus (McGuire et al. 2007, 2009). These four species breed in the United States and Canada. In contrast, courtship displays for Volcano (S. flammula) and Scintillant (S. scintilla) hummingbirds of Costa Rica are only known from the brief descriptions by Stiles (1983), and are entirely unknown for the Glowing-throated Hummingbird (S. ardens) of Panama.

Members of Selasphorus and the related genera of Calliope, Archilochus, and Mellisuga perform dynamic and spectacular courtship dives (Clark 2006, Clark and Feo 2008, Feo and Clark 2010). Selasphorus and Archilochus also produce shuttle displays for females (Banks and Johnson 1961, Hamilton 1965, Hurly et al. 2001, Feo and Clark 2010). The sounds produced during these displays are either vocal (Clark 2006), or mechanically produced with their wings and/or tail (Clark and Feo 2008, 2010; Feo and Clark 2010).

Male Scintillant and Volcano hummingbirds have emarginated inner rectrices (Fig. 1) that may function to produce sound during displays (Stiles 1983), and male Scintillant have an emarginated P10 that may produce a wing trill (Stiles 1983). Our objectives in this paper are to: (1) describe the courtship displays and sounds of Volcano and Scintillant hummingbirds, and (2) provide natural history observations of their breeding biology.

METHODS

The Volcano Hummingbird presently has three recognized subspecies: S. f. flammula, S. f. torridus, and S. f. simoni (Stiles 1983). Most of our field work on this species was conducted on S. f. torridus in open fields and pasture surrounded by oak (Quercus spp.) forest near Estación Biológica Cerro Cercado (09°33' 11.90"N, 83°40' 18.37"W; 2,600 m asl) and in Buenavista páramo habitat near km 89 on the Pan-American highway, east of San José (09°33' 20.48"N, 83°45' 18.63"W; 3,450 m asl) in the Cerro de la Muerte, Talamanca Mountains, San José Province, Costa Rica. We made additional observations and one sound recording of S. f. flammula on the summit of Volcán Irazú, Cartago Province (09°58' 34.78"N, 83°50' 57.63"W; 3,340 m asl) on 22 October 2009. We made observations of S. scintilla and S. f. torridus at the Quetzal Education and Research Center (QuERC) in San Gerardo de Dota (09°33' 15.55"N, 83°45' 18.37"W; 2,600 m asl) on 18 October 2010.
We obtained high-speed videos of hovering and displaying hummingbirds with a hand-held monochrome high-speed camera (MIRO EX4, Vision Research, Wayne, NJ, USA) recording at 500 fps with a resolution of 800 × 600 pixels. We obtained sound recordings using a shotgun microphone (Sennheiser MKH70, Wedemark-Wennebostel, Germany) attached to a 24-bit recorder (Sound Devices 702, Reedsburg, WI, USA), sampling at 48 kHz. Recordings were imported into Raven 1.3 (www.birds.cornell.edu/raven) and converted into spectrograms using a 512-sample window (Hann function, 50% overlap), except where otherwise indicated. Acoustic frequencies and temporal rates presented represent the frequencies recorded by the microphone and were not corrected for Doppler shift caused by the birds' velocity.

We captured hummingbirds with either mist nets (24-mm mesh) or feeder-traps. Some recorded sounds were natural, and the remainder were elicited by placing a live female in a cage on a male's territory, or by releasing a recently-captured female onto a homospecific male's territory. Volcano females were released on a male Scintillant's territory a few times, due to a scarcity of Scintillant females, but failed to elicit a response. We collected tail feathers for laboratory experiments, and we opportunistically obtained dive recordings from one male Volcano Hummingbird both before and after plucking his entire tail. More extensive manipulations of wild birds (as in Clark and Feo 2008, 2010; Feo and Clark 2010) were unfeasible as these experiments typically take a few weeks. Tail feathers from each species were tested in a wind tunnel to ascertain if they were capable of producing sounds similar to the dive sound. This tunnel will be described in a future publication. All measures are mean ± SD. Specimens associated with this research have been deposited in the Peabody Museum, Yale University. Sound recordings have been deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, USA (accession # 14752), and videos have been deposited in the Macaulay Library (accession #'s ML65124 to ML65144), Cornell University, Ithaca, New York, USA.

RESULTS

Volcano Hummingbird

Breeding and Territorial Behavior.—We saw females gathering nesting material and located two active nests with females incubating eggs at Cuerici on 15 October 2009, indicating breeding
was underway at this locality. Neither nest appeared to be on a male territory. Males at Cuerici held densely packed territories in open shrubby pastures full of cultivated blackberry (Rubus spp.), near remnants of oak (Quercus spp.) forest. No territories were found in closed canopy forest, although both males and females visited flowers in these areas. Males at the páramo site held small territories at the crest of a hill. Territories were small with perches of males being within a 15 × 15 m area, and central perches of neighboring territories as close as 20 m. They were tightly packed as compared to related species (CJC, pers. obs.). The males perched in 3–10 prominent locations, such as power lines, tips of dead twigs protruding from the side of a lone tree, or the tip of the tallest cane within a bramble patch while on territory. Perches were 1 to 15 m from the ground, and tended to be in sunny locations. Males at times moved to shaded perches in rare periods of prolonged sun and elevated temperatures.

Most interactions we observed on the territories were between males. Intruding males would frequently fly onto another’s territory. The owner would leave his perch and chase the intruder. The chase would often, due to the tight packing of territories, immediately encroach on a neighboring territory, and that bird would join the chase as well; if the chase then entered yet another male’s airspace, he too would join the fray. The greatest number of birds we observed in such a chase was four, accompanied by a tremendous twittering. Males seemed most active on their territories when it was sunny, and arrived on their territories within half an hour of sunrise. In contrast, they departed their territories up to 2 hrs before sundown.

All territories had at least a few plants in flower from which we saw the birds feed. The males were often visiting Fuchsia paniculata, cultivated Rubus spp., Comarostaphylis arbutoides, and the tiny flowers of F. microphylla on their territories at Cuerici. Both males and females were also observed visiting a dense patch of undefended Centropagom spp. in the understory of nearby oak forest. Males and females at San Gerardo both defended territories around small dense patches of flowering F. paniculata with both attacking other S. flammula as well as S. scintilla that intruded onto a territory. Territorial females at San Gerardo (2,200 m asl) were not observed engaging in any behaviors that would indicate breeding, such as gathering nesting material.

Vocalizations.—Males uttered a ‘descending’ call (Fig. 2A) as well as a twittering ‘scolding’ call (Fig. 2B) in agonistic interactions with other Volcano Hummingbirds. The calls produced were directed towards another individual; we did not observe undirected vocalizations (i.e., songs) from males on their territories. The descending call was also occasionally emitted towards (caged) females. It consisted of a single tone that started at 9.9 ± 0.41 kHz, and descended to 6.8 ± 1.4 kHz over the course of 1.9 ± 0.6 sec (n = 15 calls from 7 males).

Display Dives.—Males were frequently observed performing display dives throughout the day. Two of the males we observed would dive at a variety of passerine birds, if they perched prominently on the male’s territory, as well as other hummingbirds. Most males did not seem to be so indiscriminate, and were only observed diving to other Volcano Hummingbirds. It was often not possible to ascertain the gender of the recipient of the display. It was easy to elicit dives from male Volcano hummingbirds by placing a caged female on the male’s territories; the majority of males responded to this stimulus by performing at least one dive.

We obtained sound recordings of 87 dives from 13 males. The dive sound consisted of two sounds: a frequency-modulated (FM) tone and a series of sound pulses (Fig. 2C). Males began producing the FM tone early in the dive, which at its initial frequency was 4.07 ± 0.21 kHz (n = 85), and it remained nearly constant pitch (acoustic frequency) for 0.43 ± 0.17 sec. It was then modulated up to 5.80 ± 0.34 kHz (n = 87) over the course of 0.05 sec, then gradually descended in pitch to a final frequency of 4.97 ± 0.31 kHz. The entire sound lasted 0.92 ± 0.20 sec (n = 85), and a harmonic was present in 85 of 87 dives. The FM tone was clearly not produced by the tail, for one male lacking his tail still produced this sound when diving (Fig. 2E).

The dive sound also included 2–5 pulses of sound (indicated by p in Fig. 2C). These pulses were produced at the bottom of the display, as the male flew over the target of the display (Fig. 2C), and lasted 17 ± 11 ms (n = 76). The pulses were produced 46 ± 9 ms (n = 73) apart; the overall rate at which these pulses were produced was 15.2 ± 1.2 Hz (n = 76).

Each pulse consisted of a broad-frequency swath of sound reaching up to ~12 kHz. A low fundamental frequency (0.82 ± 0.29 kHz, 66
dives from 12 males; arrow in Fig. 2C) was present in 66 of 76 recordings. The sound appeared as a stack of many closely-spaced harmonic frequencies when analyzed using a spectrogram bin size of 2,048 samples (3 dB filter bandwidth: 34 Hz). The absence of the low frequency tone in 10 of the recordings may have been due to recording quality, such as recordings obtained further from the bird.

Dive Kinematics.—A male Volcano Hummingbird began a dive by ascending steeply with a slightly undulating trajectory (Fig. 3A). After rising ~25–30 m, he would turn and immediately dive, following a J or L-shaped path. After leveling out at the bottom of the dive, the male would use the accumulated speed to fly in a random direction, curving to the left or right, or up. If he performed a second dive, the male would
FIG. 3. Kinematics of display dive of the Volcano Hummingbird. (A): sketch of the dive with stages 1-3 labeled. Subsequent dives followed the same trajectory as the first dive. (B) and (C): composite images of diving birds from high-speed video. Consecutive images occurred 0.02 sec apart. Bird placement is approximate in both images, because the camera panned to follow the bird. (B): early in the dive in which the bird flapped its wings as it entered the frame (1.), then glided (2.), then spread its tail (3.) just as it left the frame. (C): the bottom of the dive in which the male spreads his tail multiple times (arrows).

re-ascend to the same starting position, and follow the same trajectory as the first dive, except for the variable ending (Fig. 3A). As a result, in consecutive dives the male passed over the recipient from the same direction. The direction of the dives did not seem to be specifically oriented towards the sun or another environmental feature that we could identify.

We obtained high-speed videos of parts of 15 dives, from seven different males. No single video showed the entire kinematic sequence of the dive. We identified stereotypical stages that appeared to be present in all of the dives by comparing the different videos. Each video was unique, thus sample sizes for each kinematic stage vary. Males descended in stage I (Fig. 3B) on flapping wings (n = 8 videos). They then ceased flapping and glided with tail shut (stage 2) for 0.17 ± 0.07 sec (n = 4 videos), before repeatedly spreading and shutting the tail while continuing to glide (stage 3; Fig. 3C). The tail was spread for 42 ± 9 msec (n = 15 spreads) and, from seven videos that showed more than one spread, the tail-spread frequency (the rate at which the tail was spread and shut) was 14.5 ± 1.6 Hz, which was not different from the sound pulse frequency (t-test, P = 0.31).

Male Volcano Hummingbirds during the dive had a wing-beat frequency of 58 ± 1.1 Hz (n = 5 high-speed videos from 2 males). A caged male had a wing-beat frequency of 66.7 Hz, while a male hovering in the wild had a wing-beat frequency of 46.9 Hz; thus, the dive wing-beat frequency is within the range observed for hovering birds. Two caged females had a hovering wing-beat frequency of 42.7 ± 0.52 Hz. The wings did not make an audible wing trill during flight, and we did not observe any displays similar to the shuttle display of other Selasphorus.

We observed one or two male S. f. flammula perform about four dives on 21 October 2009, on the summit of Volcán Irazú, of which we obtained a sound recording from one individual. We did not detect dramatic differences in the dive trajectory from the kinematics described for S. f. torridus (Fig. 2), nor did we detect notable differences in the dive sound.

Scintillant Hummingbird

Breeding and Territorial Behavior.—We heard the wing trill of Scintillant Hummingbirds near food plants at Cuérrici (2,600 m asl), and one male was collected at this location. We did not make
any behavioral observations of this species at Cuereci, and found no evidence of breeding at this location.

Scintillant Hummingbirds were breeding at San Gerardo (2,200 m asl). We observed females gathering nesting material and a female incubating a nest in a low bush on 13 October 2009. The nest did not appear to be on or near a male territory.

Males held territories in open areas such as the edge of an apple (Malus spp.) orchard, in a dense stand of blooming Fuchsia paniculata, or in short trees flanking a parking lot. All territories were in open areas, and males perched in 3–5 prominent locations between 2 and 15 m above the ground, on objects such as power lines, tips of dead twigs protruding from a large tree, on the tops of banana (Musa spp.) leaves, or the upper-most branches of a heavily blooming Fuchsia. All male territories contained at least a few plants in flower, and one included a hummingbird feeder.

The size of a territory varied depending on the amount of available food. Three males held densely-packed territories in a thick patch of blooming F. paniculata with all of the male’s perches in a roughly 10 × 10 m area. These territories were also immediately adjacent to feeding territories held by both male and female Volcano Hummingbirds. Four territories found elsewhere, in areas with fewer natural food resources and fewer neighboring territories, were roughly 25 × 25 m in extent.

Natural dives were performed to female Scintillant Hummingbirds, or to hummingbirds of unknown gender. A female Scintillant repeatedly visited flowers on a male’s territory during a set of natural observations spanning ~5 min. The male performed two sets of three dives to the bush into which a male had pursued an unidentified hummingbird. In the second variant, males (n = 2) that spotted a female crossing their territory would leave their perch and pursue the female, but not at their top speed. In this traveling shuttle, as they followed the female, the males would occasionally produce the shuttle display sound, visually appearing to decrease their forward flight speed and change their wing beat kinematics as they did so.

We obtained five sound recordings from two males performing the shuttle display (Fig. 4D). Males produced similar sounds during the traveling and stationary variants of the shuttle display. The shuttle display sounds consisted of repeated sounds that appeared in alternating duplets. One pair of sounds matched the acoustic form of the male’s wing trill (i.e., sound pulses with a mean acoustic frequency of 9.4 ± 0.43 kHz and a frequency bandwidth of 1.87 ± 0.28 kHz; n = 5; labeled w in Fig. 4D). The alternate duplet (s in Fig. 4D) was a broad-band sound without a single discrete frequency. The trill rate was 93 ± 5.1 Hz (n = 5).

High-speed videos of four shuttle displays from one male were recorded. The male was partially obscured behind other objects or, at times, out of frame throughout most of the videos, and sample sizes of specific events vary. The male flapped his wings at 98.1 ± 2.64 Hz (n = 4 displays) during the shuttle display, while rhythmically moving his body. We term each repeated, rhythmic move-
FIG. 4. Spectrograms of sounds produced by Scintillant Hummingbirds. (A): two types of vocalizations, a and b. Wing trill (w) of male is also present. (B): wing trill (w) produced by adult males. A faint harmonic is present. (C): dive sound consisted of the wing trill (w), an additional trill (T2), a harmonic of the additional trill, and a sound pulse (p). At least four sound pulses are present. The pulses are produced at the bottom of the dive, as the male passes over the female. (D): a stationary shuttle display to a female in a cage, which consisted of alternating duplets of sounds. One duplet comprises the wing trill (w), alternating with duplets of sound a that are broadband.

ment an individual 'shuttle motion'. Twice, the stationary shuttle display was performed to a female in a cage; with gorget flared, the male shuttled from side to side (laterally) in front of the cage, over a horizontal distance of ~20 cm. The male would abruptly roll his body (i.e., rotate around his longitudinal axis) while arresting his lateral motion at the end of each shuttle, flap his wings with asymmetrical motions, and sweep his tail sideways through a range of angles. The wings did not appear to strike each other or anything else, during these motions.

The other two high-speed videos were of the traveling shuttle display. Unlike the stationary shuttle, in which the male tended to fly side-to-side (laterally) repeatedly through the same space, during the traveling shuttle, the male was continually flying forward towards the female with little lateral motion. During this forward flight the male engaged in periodic body rotations, tail rotations, and asymmetrical wing kinematics similar to the stationary shuttle display (Fig. 5A). Shortly after finishing one shuttle motion, the bird would start another, rotating its body and tail in the opposite direction from the previous. The total time spent rotating the tail was 73 ± 9 msec (n = 5 shuttles from 2 videos); the timing between shuttle motions was 55 ± 13 msec (n = 2 intervals). Therefore, the rate at which shuttle motions were performed was 7.8 Hz. No component of the shuttle sound was produced at a rate of 7.8 Hz, and this striking visual component of the display kinematics did not appear to correspond to production of a single particular sound.
Display Dives.—Male Scintillant Hummingbirds would approach a caged female, but this did not elicit dives \((n = 3\) males), similar to territorial male Allen’s and Rufous \(\text{CJC, pers. obs.}\). We recorded natural dives from one male, and elicited dives from two males by releasing a Scintillant female on territory. The male would perform a shuttle display, followed by 1–6 dives, to females that landed in his territory. We recorded sounds of 17 dives from three males.

The primary audible sound during the dive was the sound of the wing trill. Two additional faint sounds were present within several sound recordings \(\text{Fig. 4C}\). The dive began with the wing trill produced at a rate of \(92.5 \pm 1.9\) Hz \((n = 17)\). There was a gap lasting \(0.32 \pm 0.12\) sec in production of the trill early in the dive for seven of 17 dives. Two to six faint pulses \(\text{(p in Fig. 4C)}\) of sound were produced \((n = 7\) dives) at the bottom of the dive at a temporal rate of \(16 \pm 2.7\) Hz \((n = 7)\). An additional trill appeared \((\text{trill 2 in Fig. 4C)}\) at the same time these pulses were produced with an average pitch ranging from 5.3 to 5.4 kHz and a bandwidth of 0.76 kHz \((n = 16)\). Trill two had a harmonic that was slightly higher in pitch than the wing trill.

Males began a dive by ascending on a slightly undulating path to a height of \(-25\) m \(\text{Fig. 5B)}\). The male would then turn and dive at a steep angle, swooping directly over the female and then rise again, tracing a giant U. At the end of the first dive the male would then turn and perform the next dive, following the same path but in the opposite direction from the previous dive, in the same vertical plane.

We obtained high-speed videos of part of four dives from two males. All lost the bird partway through the bottom of the dive. Males began the dive by powering their descent with flapping wings \(\text{stage 1)}\). Males continuously flapped for the entire dive in three dives while in the fourth the male briefly switched to a glide \(\text{stage 2)}\). Males repeatedly spread and shut their tail at the bottom of the dive while continuing or resuming...
flapping. The males spread the tail four times in two videos, and two times in the other two videos. The videos looked similar to those shown for the Volcano Hummingbird in figures 3B–C, except the wings were flapped at the nadir of the dive. The tail was spread for an average of 37 ± 2 msec (n = 7 spreads), and the intervals between spreads were 31 ± 3 msec (n = 6), resulting in a tail spread cycle rate of 14.7 Hz—corresponding to that at which the pulses of sound were produced. The gliding phase (stage 2) apparently explains the gap in production of the trill during the dive in some of the dive recordings. The dive wing beat frequency was 93.7 ± 0.66 Hz, matching the wing trill rate during the dive. Two male S. scintilla had a mean wing-beat frequency of 68.9 ± 7.6 Hz while hovering in a cage.

The R2 of both the Scintillant and the Volcano hummingbirds, when placed in a wind tunnel at speeds of 10–20 m/sec, produced sounds at the same frequencies as the pulsed sounds that the birds make while diving (Fig. 2D). The feathers generate tones with a fundamental frequency ranging from 0.3 to 0.5 kHz (depending on air speed), but in which the second or third harmonic is dominant. The feathers in the wind tunnel generated a stack of 20 or more harmonics, similar to the broad swath of sound present in the sound pulses (Figs. 2, 4). In particular, the emarginated tip of the feather flutters to generate the sound.

**DISCUSSION**

Our observations provide new information about the natural history of Scintillant and Volcano hummingbirds. The shuttle display of the male Scintillant, and dive displays produced by both species appear to be courtship displays. We saw males of both species naturally display to females, when a female was on a male’s territory. Males rarely displayed to other males, tending to chase or ignore them instead. Our experimental use of homospecific females was sufficient to immediately elicit displays from males, whereas S. flammula females released on a S. scintilla’s territory were ignored.

Our goal in conducting this research was to investigate whether *Selasphorus* species produce sounds with their wings and tail feathers. The tonal, FM portion of the Volcano Hummingbird’s dive sound is not produced by the tail (Fig. 2E), and is likely vocal. In contrast, the pulses of sound produced during the dive of both species are timed to the rapid tail-spreads in both species. We found similar one-to-one correspondences between kinematics and tail-generated sounds in Anna’s (Calypte anna), Black-chinned (Archilocus alexandri), and Calliope hummingbirds (Clark and Feo 2008, Clark 2009, Feo and Clark 2010). Moreover, the emarginated R2 (Fig. 1) of each species can generate sounds matching the dive sounds when placed in a wind tunnel (Fig. 2D). Rufous and Broad-tailed hummingbirds produce similar sounds during their dives, and both of these species also have emarginated inner rectrices (Stiles 1972, 1983), similar to Volcano and Scintillant hummingbirds (Fig. 1). We hypothesize that all of these species produce similar sounds during their dives via fluttering of the emarginated tip of R2.

There is also a one-to-one match between video and sound recordings of the Scintillant Hummingbird’s shuttle display. Sound elements w and s were produced cumulatively at a rate of 93.8 ± 5.1 Hz, closely similar to the measured wing-beat frequency of 98.1 ± 2.64 Hz. We conclude that w and s are produced by the wings, but how this is done is unclear for two reasons. First, although the individual shuttle motions of the shuttle display were periodic, they were produced at a frequency of 7.8 Hz. This is nearly four times slower than the rate of 27.8 Hz (the rate at which a cycle of a w duplet and s duplet were produced); thus, four cycles of such sounds were produced during each shuttle motion. We did not discern specific wing motions associated with the s elements. Second, the s elements are so short in duration that the sound spectrogram is intrinsically of limited use in detecting if they are truly atonal (broadband), or whether they represent a stack of closely-spaced harmonics, like the sound pulses of the dives. If they are harmonic stacks, perhaps they are produced via some form of resonant flutter (Clark and Feo 2008). If they are truly broadband, this would suggest they are produced by another mechanism such as percussion (Bostwick and Prum 2003) or rubbing (Bostwick 2006).

The function of male Volcano Hummingbird territories is not entirely clear. Wolf and colleagues (Wolf 1976, Wolf et al. 1976) called them feeding territories, implying that males were guarding a space specifically according to the value of the food resources it contained. But, food resources seemed nearly ubiquitous at our study sites, such that it would be difficult to find an open space that did not have some food present.
Thus, the presence of food on a territory is not evidence that it is a feeding territory. Some of the densest food resources (blooming *Fuchsia, Centropogon*) that occurred in closed canopy appeared to be undefended, whereas we only observed territories in open areas. In the related Anna's and Calliope hummingbirds, males will hold breeding territories in the absence of food (Tamm 1985, Armstrong 1987, Powers 1987, Tamm et al. 1989), and even those holding a territory with food resources tend to have less food available than nearby undefended locations (Armstrong 1987). We suggest that breeding male Volcano Hummingbirds are not guarding territories for the floral resources that they contain.

Males could also hold territories to guard resources other than flowers, such as insects (for which females have high demand when breeding) or nesting sites. Females did not seem to nest on male territories. It is possible they visited territories of males to obtain resources such as nectar or insects (Temeles and Kress 2010), but we made no direct observations that would support this idea. Our interpretation of the Volcano Hummingbird’s territoriality is that males need open areas to perform the display dive, and the primary function of the territory is courtship, making the mating system most similar to an ‘exploded’ lek.

The function(s) of the territories of male Scintillant Hummingbirds were less clear. The six males we found all had ample food resources on their territories, and defended their territories from Volcano Hummingbirds (nectar competitors) and male Scintillant alike, similar to the interspecific territoriality of breeding male Anna's and Allen's hummingbirds (Pitelka 1951). Moreover, a female was seen extensively feeding on one of these territories, although she did not appear to reside there. These observations suggest that resources have a role in the territory ownership of these males, perhaps more so than for Volcano Hummingbirds.

However, as for the Volcano Hummingbird, all six of these territories were held in open areas. Dense patches of flowers in areas with greater forest canopy cover had many male and female Scintillant Hummingbirds visiting them, but we did not detect any male territories in these closed areas. It is possible the males visiting these flowers were not holding territories but, as males of related species are known to forage away from their breeding territories (Armstrong 1987; Powers 1987; CJC, pers. obs.), we suspect the males we observed at these flowers held a territory elsewhere, and were commuting from their territories to feed. If true, we hypothesize that, as in the Volcano Hummingbird, habitat structure is more important than food availability for territory location. This hypothesis could be tested by covering or removing the flowers on male territories (e.g., Armstrong 1987) to examine if territorial behavior is maintained in the absence of floral resources. The potential difference in the importance of food on breeding territoriality between the Scintillant and Volcano hummingbirds would make for an interesting comparative study.

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LITERATURE CITED


BIOLOGY AND STATUS OF THE BLACK CATBIRD
(MELANOPTILA GLABRIROSTRIS) IN BELIZE

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ABSTRACT.—We studied the poorly understood Black Catbird (Melanoptila glabrirostris), a near threatened mimid, at Lighthouse Reef in northeastern Belize. A resident of coastal lowlands and offshore islands, this endemic species of the Yucatan Peninsula has been reported as extirpated from several localities and has declined in numbers at other sites. We found it relatively common on the larger of two islands that comprise Northern Two Cayes from 18 to 25 June 2005. It had not been reported there since first discovered at Lighthouse Reef in 1862 and was considered extirpated until we rediscovered it. The Black Catbird at Northern Two Cayes displayed fierce intraspecific territoriality and both males and females defended against aggressors. However, it exhibited no interspecific territoriality toward its nearest avian associate, the Mangrove Warbler (Dendroica petechia hryanti). It used wing-flashing in territorial defense, mating rituals, and while foraging on the ground. We estimated ~10 pairs of Black Catbirds in a 3-ha study area in the buttonwood-coconut (Conocarpus-Cocos) ecosystem but made no attempt to estimate the size of an apparently larger population in the more extensive area of coastal scrub on the remainder of the island. The defended territory of the pair studied most extensively was 100 × 25 m, centering on a buttonwood (Conocarpus erectus) grove and included numerous coconut (Cocos nucifera) trees. Received 19 September 2010. Accepted 5 January 2011.

The Black Catbird (Melanoptila glabrirostris) is a sedentary endemic to the Yucatan Peninsula and adjacent Central America. It occurs largely in coastal lowlands and offshore islands (Mayr and Greenway 1960, Sibley and Monroe 1990, AOU 1998). It is largely an edge species, partial to lowland humid and semiarid thickets and dense brush in coastal and riparian scrub but, at times, also occurs in interior forests and woodlands.

Several species of woody plants are important to the Black Catbird and affect its distribution ecologically and geographically. Morgenthaler (2003), in a study at Shipstern Nature Reserve, Belize found the species nesting in littoral vegetation, largely red mangrove (Rhizophora mangle), black mangrove (Avicennia germinans), and sapodilla or sapote (Manilkara zapota).

The species has been an enigma since its discovery in the mid-1800s. Almost every facet of this poorly studied species’ distribution, status, and life history has been problematic. The historic record for the species contains uncertainties and contradictory statements, dating to the question regarding the actual location from where the type specimen was taken. Originally reportedly from Honduras (AOU 1998), the species has not been recorded there since. Specimen and literature records suggest the species was not widely common although it has been common or abundant in scattered, local populations (Wood et al. 1986, Garcia et al. 1994, Jones and Valley 2001). It was apparently extirpated from several localities where it was formerly recorded during the late 1800s and early 1900s, e.g., Lighthouse and Golvers reefs, but was not found subsequently (Russell 1964, Jones and Vallegy 2001, Jones 2005). It was recorded early (Salvin and Goodman 1879, Russell 1964) at Northern Two Cayes (NTC) and Half Moon Caye, islands on Lighthouse Reef (LHR). The species was not found later at NTC by Bird (1954) or at Half Moon Caye (Vernor 1961, and pers. comm. to S. M. Russell; Meerman 1996). The Black Catbird was considered extirpated at NTC (Jones and Vallegy 2001; Jones 2005; S. M. Russell, pers. comm.) until we rediscovered the species there in 2005.

Many ornithological papers for the region have largely ignored the species despite evidence of declining populations. This decline was suggested early for Belize by Russell (1964) who reported the Black Catbird had not been recorded there between 1931 and 1964. Others have indicated uncertainty of its status by use of question marks (Phillips 1986, Howell and Webb 1995).

The Black Catbird was described by Sclater in 1858 (AOU 1998). The type specimen was labeled Omoa, Honduras but the species has not since been recorded from that country. Most references question the Omoa record (Phillips 1986) and consider the probability the type specimen was taken in British Honduras, now Belize (Monroe 1968, Ridgley and Gwynne 1989).

Most consider Melanoptila a monotypic genus with one subspecies (Phillips 1986). A second
subspecies, *M. g. cozumelana* (Paynter 1954), was named from Cozumel Island, Quintana Roo, Mexico and has been, at times, listed (Miller et al. 1957, Mayr and Greenway 1960). The species has been, at times, placed with the closely related Gray Catbird (*Dumetella carolinensis*) as *D. glabrirostris*; (Paynter 1954, 1955b: Land 1970). The two resemble each other in behavior and appearance, except for color, and the eggs of the two species are almost identical (L. F. Kiff, pers. comm.). A recent molecular systematic analysis of Caribbean mimids continued to treat the two genera separately (Hunt et al. 2001).

Nothing was known about its breeding season until the mid-1900s when a male with enlarged testes was taken in Quintana Roo (Paynter 1955a) and two males and a female in breeding readiness were taken on Isla Cozumel (Klaas 1968). Us breeding biology was basically unknown until recently and we find no studies that have examined the complete natural history of the species, or its behavior. We know of only two unpublished theses, one for Belize, in English (Morgenthaler 2003), the other for Mexico, in Spanish (Roldán Clará 2009), and two AOU annual meeting abstracts of Black Catbird breeding studies (LaPergola et al. 2009, Roldán Clará et al. 2009).

In addition to our observations of the Black Catbird at NTC, we added information from the literature, on-line, and discussions with other experienced individuals. We also physically searched through the libraries of The Peregrine Fund, Boise, Idaho; Denver Museum of Nature and Science, Colorado; and University of Arizona, Tucson.

Our objectives in this paper are to: (1) report the occurrence of a Black Catbird population in a locality where it had not been found since 1862 and was considered extirpated (Russell 1964, Jones and Valletty 2001, Jones 2005); (2) document previously unreported territorial, foraging, and related behavior; and (3) emphasize the apparent diminishing of the species populations, especially in Belize (Russell 1964; Miller and Miller 1991, 1998; Collar et al. 1992, 1994; Stattersfield and Capper 2000; Jones and Valletty 2001; Jones 2005).

**METHODS**

Most of our study was conducted at Lighthouse Reef Resort (LHR) on the larger island of Northern Two Cayes (NTC). This and a much smaller island comprise NTC and are the northeasternmost islands on LHR. The smaller island is almost entirely covered by a lighthouse operation and coconut (*Cocos nucifera*) plantation. We found the Black Catbird relatively common in disjunct hawthorn (*Conocarpus erectus*) thickets and undertook a study of its habitat, territoriality, behavior, and other factors from 18 to 25 June 2005. We estimated ~10 pairs of Black Catbirds in a 3-ha study area in the hawthorn-coconut ecosystem but made no attempt to estimate the size of the population in the most extensive area of coastal scrub on the remainder of the island. We calculated territory sizes and related factors from on-ground measurements and estimated gross measurements (e.g., total study area, areas on Half Moon Caye, etc.) by extrapolation from on-site measurements applied to Google Earth imagery.

Observations were made from windows of a LHR Resort cabin and on the ground. Information regarding territorial behavior was recorded at the boundary between two territories in a large hawthorn thicket adjacent to the cabin. A large hawthorn tree ~10 m from our cabin window, allowed easy viewing. The perch most often used by catbirds was on this tree’s trunk, which was ~20 cm in diameter, 3.5 m from the base of the tree. The tree had been severely bent by onshore winds and the perch was <1 m above the ground, allowing birds to easily move back and forth along the trunk that was almost parallel to the ground. This was a favorite perch of territorial pair A at the edge of their 0.25-ha territory, but was often visited by pair B from the adjacent territory to the west. Two to three (rarely 4) catbirds often interacted on this trunk which was sufficiently flat to provide a platform for mating displays and territorial battles.

We did not find the Black Catbird at Half Moon Caye National Natural Monument despite finding numerous hawthorn tree thickets along the waterfront. This is one of the three islands on LHR, besides NTC, where the species occurred in the past (Salvin and Goodman 1879, Russell 1964). Trunks of large coconut trees and other woody debris littered the waterfront, suggesting more recent and/or more severe hurricane damage than at NTC. We also failed to find the species in the coastal lowlands near Belize City, an area from which it had been previously reported (Young 1974, 1981).
RESULTS

Territoriality.—The Black Catbirds on NTC spent most of the time out of view in thick buttonwood groves. Territorial males were fiercely defensive when in the open on the ground or in sparse vegetation and seldom allowed other catbirds or a person to approach any closer than 10-15 m. They challenged other catbirds that intruded on their territories, pursuing them on the ground, in the air, and through vegetation. Although demonstrating strong intraspecific territoriality they showed no interspecific territoriality toward the Mangrove Warbler (Dendroica petechia bryanti) or White-crowned Pigeon (Patagioenas leucocephala), the only two other avian species occurring regularly in the buttonwood-coconut ecosystem on NTC. The White-crowned Pigeon, also a near threatened species (IUCN 2010), stayed high in the crowns of coconut palms, above catbirds, but a male Mangrove Warbler commonly fed within 2 m of a Black Catbird without signs of aggression by either species.

Buttonwood groves were widely scattered on our 3-ha plot. The defended territory of the pair (A) studied most extensively was 100 × 25 m, centered on a buttonwood grove and including numerous coconut trees. Little herbaceous vegetation grew in sandy soil between the coconut palms and buttonwood trees other than seashore spiderlily (Hymenocallis littoralis). There were no Black Catbird territories to either side of territory A and none to the east, but a territorial pair (B) often threatened from the west. When followed, catbird A would fly ahead of us to the east beyond its 100-m territorial edge by ~25 m and, when it chased intruder B, it would fly 15-20 m past its western territorial edge. Thus, the entire length of area occasionally used by pair A was ~140 m.

We could only assume that most aggressive interactions between two or more Black Catbirds were generally between males due to the lack of sexual dimorphism. However, on one occasion, four Black Catbirds became involved in a squabble that lasted ~3 min in and around the favored buttonwood. At the end of the squabble, after two catbirds (apparently pair B) had flown west, the two remaining Black Catbirds (apparently pair A) faced each other on the bent buttonwood trunk ~60 cm above the ground. Both remaining birds did partial wing-flashes with both wings, while spreading their tails; one then flew toward the center of the territory. The remaining catbird flew to the ground, did a full wing-flash and followed in the same direction.

Perches and Singing Posts.—The Black Catbird usually remained within 2 m of the ground except when singing, often hopping from the ground onto a low stump or leaning tree trunk, then back to the ground again. It often sang from a prominent, open perch such as a stump, base limb of a tree, or occasionally near the top of a medium-sized coconut tree, usually 8 m or less in height. Rarely, they sang from within tree crowns, e.g., at least three individuals remained hidden from view while singing in a dense buttonwood grove at ~1130 hrs on 24 June.

Wing-Flashing and Tail-Fanning.—The Black Catbird used both partial and full wing-flashing, raising its wings part way or fully extending them similar to that of the Northern Mockingbird (Mimus polyglottos). Occasionally a catbird would raise only one wing. We noted the Black Catbird wing-flashing during territorial battles, while foraging, and toward a presumed mate. Tail-fanning also, at times, accompanied wing-flashing, similar to that of the Gray Catbird. A Black Catbird on the ground often engaged in wing-flashing when confronting an intruder. A chase on foot might follow after a wing-flash before the intruder took flight, followed by the territorial bird.

Foraging and Food.—The Black Catbird at NTC foraged extensively among the debris under buttonwood trees. One would stop to flick debris aside with a sideways movement of its bill then move forward a meter or less and repeat the action in a manner similar to the Gray Catbird. Occasionally, on stopping, the catbird would do a double wing-flash before tossing leaves aside. They were apparently feeding on invertebrates (e.g., insects and spiders) since we could find no edible vegetable material among the leaves and dried buttonwood fruit. The only seeds to be expected would be tiny buttonwood seeds.

We observed a Black Catbird feeding frantically on the ground in the buttonwood grove ~10 m outside our cabin window at 1005 hrs on 24 June. After ~1 min it flew to the adjacent favored buttonwood and another catbird, apparently its mate, flew to the ground and fed for ~1 min more at the same spot then joined the first in the favored buttonwood. Close examination of the area showed that ants were carrying termites and termite eggs from a broken termite tube to their nest and the two catbirds had been feeding on ants and/or termites.
DISCUSSION

The time of year Black Catbird breeding occurs on NTC is unclear. The catbirds we studied were extremely territorial. Pair A displayed courtship behavior but we saw no copulation, nesting, feeding of young, or newly fledged young for any pair. Breeding is from May to August both in Quintana Roo, Mexico (LaPergola et al. 2009) and in the Shipstem Nature Reserve in northeastern coastal Belize, where maximum nesting occurs in June (Morgenthaler 2003).

Territoriality.—The catbirds at NTC allowed no other catbirds in their territories but studies at other localities report different results. Extreme territorial defense is either not typical in some Black Catbird populations or lessens during the nesting season. Black Catbird breeding studies in the Shipstem Nature Reserve indicated ‘‘they do not express a very strong territoriality’’ (Morgenthaler 2003:24). Nests there were mostly 20 to 40 m apart but occasionally <20 m apart (Morgenthaler 2003). ‘‘Several concurrently active nests were <3 m apart’’ in Quintana Roo (LaPergola et al. 2009:66).

Wing-Flashing and Tail-Fanning.—The function of wing-flashing is not fully understood but is used by the Black Catbird and several other species, including several mimids. It may be used in aggressive behavior (e.g., territorial display and to frighten predators), foraging (to startle insects), and during mating rituals (Selander and Hunter 1960, Terres 1980, Derrickson and Breitwisch 1992). One of the more noted cases of wing-flashing is in the Northern Mockingbird. (Selander and Hunter 1960, Derrickson and Breitwisch 1992). Tail-fanning, similar to that illustrated for the Gray Catbird by Cimprich and Moore (1995), was a display that at times accompanied wing-flashing by Black Catbirds at NTC. Tail-fanning was especially noted during courtship rituals at NTC but a study by Jablonski (1999) also found it increased flushing and capture of arthropods. Tail-fanning increased foraging success of the Painted Whitestart (Myioborus pictus), another tropical passerine, and reinforces the premise that wing-flashing and tail-fanning may serve as a successful foraging strategy in some avian species.

Important Plants.—Black Catbirds feed on both animal and vegetable matter, and plants that produce fruits on which they feed are especially important. Several plants are also important as habitat components, especially in Caribbean island and coastal lowland littoral ecosystems inhabited by the catbird. Several of these same plant species are also important as ecosystem components and for food for the White-crowned Pigeon, the second most common avian species in the buttonwood-coconut ecosystem at NTC. This pigeon has a much wider distribution than the catbird (Goodwin 1977, Bancroft and Bowman 2001), but occurs with the catbird through much of its range. Both are near threatened species (IUCN 2010), and knowledge of shared dependence on certain plant species is important (Appendix).

CONSERVATION IMPLICATIONS

Several factors, both intrinsic and extrinsic, threaten Black Catbird populations. These include: (1) habitat fragmentation, especially from tourism developments. (2) hurricanes and subsequent wildfires, (3) small clutches of two to three eggs, and (4) low fledging rates.

The species’ is listed as a ‘‘Species of Concern’’ by Jones and Vallety (2001:56) and its declining status suggests the possible need for a more critical designation than near threatened (IUCN 2010), especially for Belize and Guatemala, and possibly for Mexico. The Black Catbird is vulnerable to habitat fragmentation resulting from hurricanes and development, especially for tourism (Miller and Miller 1991, 1998; Stattrsefand and Cappe 2000; Jones and VallTe 2001; Morgenthaler 2003; Jones 2005). Deleterious impacts in Belize from development of coastal ecosystems, offshore islands, and inland wetlands are widespread. Miller and Miller (1998; 545) noted the increased avian species richness of ‘‘both resident and migrant species as well as individuals’’ in riverine riparian and coastal ecosystems in Belize. It is in those ecosystems that most development for tourism, urbanization, and agriculture is occurring.

Miller and Miller (1991) postulated that originally there was sufficient suitable habitat that when portions were destroyed by hurricanes, the species continued to exist in undamaged refuges. Catbirds from these refuges could repopulate recovering damaged areas. However, there is a lessened probability of the existence of Black Catbird refuge areas with continuing ecosystem loss and fragmentation. Fires that burn through the debris left by hurricanes are, at times, a greater threat to the Black Catbird and other
Development for tourism and urbanization does not always decimate Black Catbird populations. If patches of native vegetation remain, especially littoral vegetation (e.g., mangroves). Healthy populations of Black Catbirds currently exist on Ambergris Caye, Belize, and Isla Cozumel, Mexico, despite continuing development. A beachfront residence with a lagoon and expanding stands of mangroves on Ambergris supports a population of Black Catbirds (Dan Plunkett, pers. comm.) and, despite expanding tourism on Cozumel, concentrations of the species exist, often near golf courses where water and mangroves remain (J. O. Cornelia and S. I. Swain, pers. comm.). Another serious consideration for the Black Catbird relates to the small number of two to three nests per nest (Morgenthaler 2003, LaPergola et al. 2009). In addition, a high mortality rate of 80% for nestlings (LaPergola et al. 2009, Roldán-Clará et al. 2009) results largely from predation (Morgenthaler 2003, LaPergola et al. 2009, Roldín-Clará et al. 2009). This low reproductive potential increases the danger of being unable to recover, especially if there is a catastrophe, e.g., a severe hurricane or loss of large tracts of suitable habitat. These factors, combined with losses of coastal, island, and inland wetland ecosystems, result in a precarious situation for the Black Catbird in Belize and throughout much of its remaining range.

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<th>Plants</th>
<th>Nesting</th>
<th>Feeding</th>
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</thead>
<tbody>
<tr>
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<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Black mangrove <em>Avicennia germinans</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Buttonwood <em>Conocarpus erectus</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Sapodilla, sapote <em>Manilkara zapota</em></td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Guano Imbe, red berth <em>Bursera simaruba</em></td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Seagrape <em>Coccoloba uvifera</em></td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Black torch <em>Eriathlon fruticosa</em></td>
<td>5</td>
<td>2, 6</td>
</tr>
<tr>
<td>Poisonwood <em>Metopium spp.</em></td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Mango <em>Manilkara indica</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Hemsley wild fig <em>Ficus hemsleyana</em></td>
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<td>5</td>
</tr>
<tr>
<td>Wild fig <em>Ficus spp.</em></td>
<td>1</td>
<td>3, 5</td>
</tr>
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<td>Thatch palm, chit palm <em>Thrinax radiata</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Nightshade <em>Solomon spp.</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Firebush <em>Hamelia patens</em></td>
<td>6</td>
<td>5</td>
</tr>
</tbody>
</table>

* Species on Northern Two Cayes (after Fosberg et al. 1982).
* Trees in which nests are placed.
* Plants in nesting ecosystem.
* Fruits eaten and places of feeding (Morgenthaler 2003:18).
* Fruits eaten.
* On Half Moon Caye but not Northern Two Cayes.
* On Half Moon Caye and other islands of Lighthouse Reef but not Northern Two Cayes.
* *Solomon hodgsoni* on Half Moon Caye but no *Solomon* on Northern Two Cayes.
NEST SITE SELECTION AND CONSEQUENCES FOR REPRODUCTIVE SUCCESS OF THE ENDANGERED MARIANA CROW (CORVUS KUBARYI)

RENEE ROBINETTE HA,1,5 JOHN M. MORTON,2 JAMES C. HA,1 LAINIE BERRY,3 AND SHELDON PLENTOVICH4

ABSTRACT.—Reasons for the decline of the Mariana Crow (Corvus kubaryi) on the Western Pacific island of Rota are currently unknown, but a need to protect nesting habitat has been suggested. We examined 55 actual nest sites and 60 random sites from 1997 to 1999 to investigate habitat characteristics specific to crow nest sites. Both nests and random plots were predominantly in limestone forest habitat. Discriminant function analyses indicate actual nest sites were differentiated from random sites based on a higher percentage of canopy cover and mean DBH of papaya (Carica papaya) and woody vines, as well as a higher stem count of species associated with limestone forests. This resulted in correct classification of a potential site as nesting versus random in 92% of the cases. Actual nests were >300 m from buildings, while random sites averaged (± SE) 226.7 ± 71.6 m from a building. Actual nest sites were about twice as far from a road as random nest sites. Twenty-eight of the 55 active nests fledged young. Nests in native forests were associated with higher reproductive success than nests in more disturbed areas. These findings suggest that damage to habitat from anthropogenic or natural causes may be limiting nesting success. Received 19 February 2010. Accepted 22 November 2010.

Some species of Corvidae appear to select nest sites to reduce risk of predation (e.g., Hooded Crow [Corvus cornix], Loman 1979; Florida Scrub-Jay [Aphelocoma coerulescens], Bowman and Woolfenden 2002), while others may select nest sites to minimize exposure of the nest to harsh weather conditions (Pinyon Jay [Gymnorhinus cyanocephalus], Balda and Bateman 1972; Brown Jay [Psilorhinus morio], Lawton and Lawton 1980). These different preferences represent adaptive responses to environmental variables (Bowman and Woolfenden 2002) to maximize fecundity.

The Mariana Crow (Corvus kubaryi) is listed as an endangered species (USDI 1984) and originally occurred only in the Mariana archipelago on two adjacent islands, Rota and Guam. It has been extirpated on Guam by the brown tree snake (Boiga irregularis) (Wiles et al. 2003). Mariana Crows can re-nest and have an extended breeding season, but the peak season appears to be October through March (Lusk and Taisacan 1996). They occasionally build multiple dummy nests prior to incubation, lay 1–4 eggs, and typically fledge 1–2 young (Morton et al. 1999). Both adults care for the young and defend the nesting territory; there is no evidence of cooperative breeding in this species (Morton et al. 1999). Little is known about characteristics of their preferred nest sites except they appear to favor primary and secondary limestone forest (Plentovich et al. 2005).

Most studies comparing nesting and random sites focus on proximate cues associated with nesting habitat, while those that use measures of reproductive success associated with nest site selection (Krebs 1994, Dunk et al. 1997). Analysis of nest site selection of the Mariana Crow has implications for conservation of its habitat; an analysis of the fitness implications of habitat selection can reveal whether some selections confer higher reproductive success (Clark and Shutler 1999). Nest site characterization involves comparing sites where birds build nests to the habitat available for nesting. This level of analysis does not necessarily reveal optimal nesting habitat, as some birds may use suboptimal sites due to lack of available habitat or inexperience (Clark and Shutler 1999). It is also necessary to compare successful and unsuccessful nest sites (successful nests produce fledglings) to discern whether nest sites are characterized by what is available or what is optimal for nest success. Our objectives are to: (1) report nest site selection by Mariana Crows using active nest sites and random sites within the same study areas, and (2) examine how successful and unsuccessful nest sites differ.
METHODS

Study Area.—This study was conducted from 1997 to 1999 on the island of Rota (14°15′N, 145°21′E), part of the Mariana archipelago in the northwestern Pacific Ocean. The island has an area of 86 km² and a maximum elevation of 491 m. It is primarily composed of limestone, but contains exposed areas of volcanic origin, and is classified as high volcanic with raised coral terraces (Falanruw et al. 1989). The ecosystem is described as rain forest on the upper terraces and grasslands and scrub on lower volcanic slopes and limestone terraces. The majority of Rota's native forest is still intact, unlike the other inhabited islands in the archipelago that are mostly deforested (Falanruw et al. 1989).

Breeding activities of Mariana Crows were studied at six sites of ~1 km² each (Morton et al. 1999). These sites were selected because they were relatively large contiguous land parcels vegetated by forest habitat types found elsewhere on Rota (cf. Falanruw et al. 1989). The relative amount of limestone forest on these six sites ranged from 58 to 96% (estimated from Falanruw et al. 1989). However, forests on these sites may be slightly more pristine than the typical forest on Rota. Secondary vegetation, consisting primarily of introduced tangantungan (Leucocena leucocephalus), comprised only 6% of the forested area of the study sites but 16% of forests on the island (Falanruw et al. 1989). Native limestone and atoll forests represent 80% of the forested area on the study sites and 72% on Rota overall.

Characterization of Active Nest Sites.—Nests of Mariana Crows were located by systematic searches of the six study sites. Nests were visited approximately once per week after activity was detected, and were examined each time with a mirror on a pole to count the number of eggs or nestlings. Nests were considered to be active if confirmed to contain eggs, nestlings or fledglings at any time. Active nests that fledged at least one young were considered successful.

Specific coordinates (UTM) were obtained with a Global Positioning System (GPS) with accuracy recorded of ±10 m. The tree species of the tree was recorded (Raulerson and Rinehart 1991), and the diameter (to the nearest mm) of the tree trunk was measured using tree calipers at breast height (DBH). Nest height was defined as the distance from the bottom of the center of the nest cup to the ground immediately below the nest (nearest cm). Tree height was measured from the base of the tree to the top-most branch (recorded to the nearest 0.1 m). The branch length of a nest was the distance measured from the nest cup to the base of the branch. Nest aspect was the compass bearing of the nest relative to the tree trunk, and was measured with the observer's back against the trunk of the tree to record the compass bearing (degrees) of a marker placed below the nest. Canopy cover was obtained by taking 12 readings with a densiometer at three locations (4 readings per location). The densiometer was placed on a tripod and canopy cover was estimated immediately above the marker placed below the nest center. Other readings were taken 5 m north and south of the nest.

Characterization of the Vegetation of Nest Plots versus Random Plots.—Vegetation surveys of nest plots were conducted around the nest tree. The structure and composition of the vegetation was characterized for 55 nest plots and 60 stratified random (12.6-m circular) plots (Fig. 1) within the same six study sites (Table 1). Random plots were located by systematically stratifying the study sites into 10 units (to capture spatial variation), and randomly drawing a plot from each of the 10 subunits. Random plots were within nest study areas; thus, they were available to birds as nest sites, but were not selected by the birds in this study. The vegetation characteristics included the number and DBH (>24 mm) of stems by species, the number and DBH of snags, canopy cover, slope, elevation, and distance and direction to edge, road or building (if <300 m). Buildings >300 m from the plot center were not recorded. Slope was measured with a clinometer at a representative location uphill and downhill from the nest tree (the 2 readings were 180° apart). The straight-line distance and direction from the plot center to the nearest road, edge, and building were recorded. Roads were classified as graded or paved; we did not include 2-wheel tracks. Edge was defined as an abrupt change in habitat such as beach strand to open beach, limestone forest to road edge, or secondary forest to open field. At times, the nearest road was the nearest edge. Plot elevations were recorded from a USGS topographic map.

Data Analysis.—Three comparisons were performed: vegetative and spatial differences between active versus random plots, differences between the six study sites, and differences between successful and unsuccessful nest sites.
We performed a discriminant function analysis (DFA) which allowed us to statistically control for numerous intercorrelated vegetative (stem and DBH) variables. All variables were included initially, and then reduced in an iterative process to identify the smallest set of predictor variables which maximized predictive power. Jack-knifed classification percentages were reported in all cases. Some variables required log transformation to meet the assumption of normality. One variable (distance to a building) could not be compared for active nests and random plots because it was not measured unless a building was within 300 m; no buildings were within 300 m of any active nest site. Variables eliminated from the DFA of successful versus unsuccessful nests due to insufficient sample size caused by some missing data were: slope, elevation, distance to road, and distance to edge. Mean stem counts and mean DBH values for each species were calculated for each sample. The average stem counts and DBH values for each species were then summed across species to form two novel variables: total number of stems per plot and sum of the mean DBH. These variables represent forest density and maturity, respectively. The genus Eugenia includes two species on Rota that are difficult to discriminate and, for the purposes of these analyses, we use the genus to collectively refer to these two species. However, E. thompsonii was easy to discriminate and was noted separately.

Dichotomous and categorical variables were analyzed with contingency table tests. The Yates correction was performed when expected cell values were <5 (Sokal and Rohlf 1981).

**TABLE 1.** Study sites and number of nests of Mariana Crows, 1997–1999.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Number of nests</th>
<th>Number of random sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duge (DU)</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Golf Course (GC)</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Lalayak (LA)</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Mochong (MO)</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td>Pali (PA)</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Rail Release (RR)</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td>Totals</td>
<td>55</td>
<td>60</td>
</tr>
</tbody>
</table>

**RESULTS**

*Descriptive Characteristics of Nest Sites.*—Tree species used by Mariana Crows for nesting on Rota included A'ahang (Eugenia reinwardtiana), Fagot (Neisosperma oppositifolia), Ifit (Ifis bijuga), and Zebra wood (Guettarda spectabilis) and were chosen significantly more often than 16 other species of nest trees ($\chi^2 = 82.94, df = 17, P < 0.001$; Table 2). The mean height of the
TABLE 2. Trees species used as nest sites by Mariana Crows, 1997-1999.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Number</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neiosperma oppositifolia</td>
<td>Hagot</td>
<td>28</td>
<td>22.6</td>
</tr>
<tr>
<td>Eugenia reinwardtiana</td>
<td>A'abang</td>
<td>19</td>
<td>15.3</td>
</tr>
<tr>
<td>Intro bigua</td>
<td>Ift</td>
<td>17</td>
<td>13.7</td>
</tr>
<tr>
<td>Guertarda speciosa</td>
<td>Zebrwood</td>
<td>13</td>
<td>10.5</td>
</tr>
<tr>
<td>Premna obtusifolia</td>
<td>False elder</td>
<td>9</td>
<td>7.3</td>
</tr>
<tr>
<td>Pouteria ohovata</td>
<td>Lalaha</td>
<td>8</td>
<td>6.4</td>
</tr>
<tr>
<td>Guettarda mariannae</td>
<td>Paipai</td>
<td>6</td>
<td>4.8</td>
</tr>
<tr>
<td>Ficus spp.</td>
<td>Fig</td>
<td>4</td>
<td>3.2</td>
</tr>
<tr>
<td>Pisonia grandis</td>
<td>Umumu</td>
<td>4</td>
<td>3.2</td>
</tr>
<tr>
<td>Unknown</td>
<td></td>
<td>3</td>
<td>2.4</td>
</tr>
<tr>
<td>Psychotria mariana</td>
<td>Aploghating</td>
<td>3</td>
<td>2.4</td>
</tr>
<tr>
<td>Cyperus reinwardtiana</td>
<td>Gulas</td>
<td>2</td>
<td>1.6</td>
</tr>
<tr>
<td>Drypetes dolichocarpa</td>
<td>Mwelel</td>
<td>2</td>
<td>1.6</td>
</tr>
<tr>
<td>Maytenus thompsonii</td>
<td>Lulujut</td>
<td>2</td>
<td>1.6</td>
</tr>
<tr>
<td>Barringtonia asiatica</td>
<td>Fish-kill tree</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>Elaeocarpus joga</td>
<td>Yoga</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>Macaranga thompsonii</td>
<td>Pengua</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>Tristiropsis obtusangula</td>
<td>Faniok</td>
<td>1</td>
<td>0.8</td>
</tr>
</tbody>
</table>

* Two species (Ficus mauritia and F. prolixa) occur on Rota.

The nest tree was 7.8 m with a DBH of 0.17 m and slope of 10.8°. The mean nest height was 5.9 m and the nest was on a branch with a mean branch length of 1.7 m.

Comparisons Between Active Nests and Random Plots.—Active nests were >300 m from any buildings, and no distance was recorded for actual nests; random sites had a mean distance of 226.7 m from a building. Nests were a mean distance of 223.9 m from a road, while random plots were 133.5 m from roads on average ($t_{23} = 1.48$, $P = 0.14$). There was no significant difference in univariate $t$-test comparisons between nest and random sites for the distance from an edge ($t_{10} = 0.32$, $P = 0.75$). There were also no significant differences between nest and random sites for characteristics of elevation ($t_{10} = 0.46$, $P = 0.65$), or slope ($t_{10} = 0.65$, $P = 0.52$).

Discriminant Function Analyses.—Forty-nine species of trees and two categories (snags and woody vines) were recorded in vegetation surveys. Discriminant function analyses indicated which variables (Table 3) resulted in a correct classification of potential habitat as an active nest site versus a random site in 92% ($F_{1,81} = 16.97$, $P < 0.001$). Active nests that were successful versus those not successful differed ($F_{5,34} = 10.12$, $P < 0.001$; Table 4). This resulted in correct classification of potential habitat as successful versus unsuccessful in 85% ($F_{1,40} = 9.56$, $P < 0.001$; Table 5), and resulted in correct classification of each study site in 71% of these cases.

### Table 3

**Measure** | **Variable** | **Active nests** | **Random sites**
|-------------|--------------|-----------------|-----------------
| Average nest cover | Carica papaya | 93.59 ± 0.95 | 83.69 ± 3.12 |
| DBH | 9.6 ± 2.10 | 0.00 |
| DBH | Cycas circinalis | 5.09 ± 3.56 | 17.30 ± 6.27 |
| # Stems | Eugenia spp. | 37.45 ± 7.00 | 24.50 ± 4.19 |
| DBH | Eugenia spp. | 25.79 ± 2.99 | 30.34 ± 2.30 |
| DBH | Eugenia thompsonii | 1.03 ± 1.03 | 2.16 ± 1.23 |
| Mean DBH | Exoecaria agallocha | 1.56 ± 1.56 | 0.00 |
| # Stems | Guettarda mariannae | 33.36 ± 8.06 | 19.92 ± 4.07 |
| Mean DBH | Guettarda speciosa | 66.74 ± 11.01 | 72.25 ± 8.85 |
| # Stems | Pandanus spp. | 7.30 ± 1.54 | 19.02 ± 4.23 |
| Mean DBH | Pemphis acidula | 0.00 | 2.22 ± 1.65 |
| # Stems | Pipturus argenteus | 2.25 ± 0.81 | 3.12 ± 0.79 |
| Mean DBH | Pipturus argenteus | 12.31 ± 3.27 | 30.29 ± 4.95 |
| # Stems | Psychotria spp. | 3.82 ± 1.21 | 6.75 ± 1.52 |
| Mean DBH | Psychotria spp. | 38.94 ± 6.28 | 48.33 ± 5.33 |
| # Stems | Randia cochinchinensis | 1.20 ± 0.27 | 1.33 ± 0.32 |
| Mean DBH | Randia cochinchinensis | 29.73 ± 4.48 | 20.77 ± 3.81 |
| Mean DBH | Snags | 35.49 ± 6.29 | 0.00 |
| Mean DBH | Tureina umbucina | 4.34 ± 2.11 | 2.86 ± 1.41 |
| Sum | Sum # Stems | 233.97 ± 20.39 | 252.62 ± 16.40 |
**TABLE 4.** Mean ± SE for DBH (cm) and number of stems (counts) of species discriminating successful from unsuccessful nests of Mariana Crows, 1997-1999.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Species</th>
<th>Successful nests</th>
<th>Unsuccessful nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean DBH</td>
<td><em>Ficus tinctoria</em></td>
<td>18.69 ± 5.56</td>
<td>32.96 ± 7.35</td>
</tr>
<tr>
<td>Mean DBH</td>
<td><em>Ochrosia mariannensis</em></td>
<td>16.17 ± 4.83</td>
<td>9.10 ± 4.72</td>
</tr>
<tr>
<td>Mean DBH</td>
<td><em>Polyscias grandifolia</em></td>
<td>10.47 ± 4.08</td>
<td>7.79 ± 3.88</td>
</tr>
<tr>
<td>Mean DBH</td>
<td><em>Pouteria obovata</em></td>
<td>56.03 ± 10.04</td>
<td>23.64 ± 10.07</td>
</tr>
<tr>
<td># Stems</td>
<td><em>Psychotria spp.</em></td>
<td>6.36 ± 2.31</td>
<td>1.44 ± 0.47</td>
</tr>
</tbody>
</table>

**DISCUSSION**

*Eugenia reinwardtiana, Neisosperma oppositifolia, Ixius bijuga,* and *Guettarda speciosa* were chosen significantly more often than 16 other species of trees used by Mariana Crows for nesting. All trees species used for nesting are native to Rota. This finding could be due to the higher proportion of these commonly used species in the forests of Rota, and does not necessarily reflect a preference for these species. There were no significant differences between nests and random plots in elevation, distance or direction to edge, distance or direction to road, slope, or total number of stems.

Mariana Crows chose nest sites that: had greater canopy cover, larger stems of papaya (*Carica papaya*), contained species associated with limestone forests, and had larger woody vines than random sites. Mean canopy cover was about 10 percentage points greater for nest than random sites. Nests were high in the canopy (mean ± SE nest height = 6.6 ± 0.3 m) but were placed, on average, 2 m below the crown (nest tree height = 8.7 ± 0.3 m). Higher canopy cover may reflect efforts to hide the nest from predators, protect the nest from the adverse effects from sun, or limit wind damage from typhoons (Bowman and Woolfenden 2002; J. C. Ha, unpubl. data).

Nest sites were also associated more frequently with larger papaya stems. Mariana Crows have been observed eating wild papaya (R. R. Ha, pers. obs.). However, it is unclear whether the importance of papaya trees suggests crows choose nest sites with papaya nearby or whether papaya trees appear near nest sites due to the consumption of papaya by crows and subsequent seed dispersal in the nesting territory. We believe the latter may be the case because closed canopy forests are poor habitat for papaya, which typically prefers disturbed soils with high exposure to sunlight (Raulerson and Rinehart 1991). Woody vines may be actively selected by Mariana Crows. Lusk and Taisnean (1996) found that one particular native vine, Marianne jasmine (*Jasminum marianum*), comprised 84% of the materials of nest platforms, and other vines and twigs were also used. Nest trees were >300 m from buildings suggesting Mariana Crows generally prefer to nest away from human disturbance. Baker (1951) and (NRC 1997) indicated Mariana Crows avoided human habitation. Roads on Rota may not be as disturbing as houses to Mariana Crows. Rota only has 3,283 residents (U.S. Department of Commerce 2000) and vehicle traffic is light.

Mariana Crows were more likely to have a successful nest on sites within the closed-canopy limestone forest with smaller *Ficus tinctoria*, greater stem densities of *Psychotria spp.*, and larger *Ochrosia mariannensis, Polyscias grandifolia,* and *Pouteria obovata*. *Ficus tinctoria* is associated with the beach or back strand vegetation, and was linked with unsuccessful nests. The other vegetation associated with successful nests is reflective of limestone forests (Raulerson and Rinehart 1991). Five of the six study sites were logged by the Japanese between 1917 and the end of WWII and the forest we surveyed is known to be 50-90 years of age. Fosberg (1960) reported that much of Rota was cleared between 1932 and 1935; by 1946, only one-fourth of the island was covered by "well-developed" forest. Older limestone forest growing on the steep slopes of the Sabana tends to have a much more open understory and much lower densities of Mariana Crows (Fancy et al. 1999, Plentovich et al. 2005). We do not believe that vegetation species linked with successful nests necessarily convey unique species-specific advantages to Mariana Crow productivity. Collectively, they describe forest composition and structure that is consistent with a maturing, undisturbed, native limestone forest in the Mariana Islands. If the forest is too young, the canopy is too open and may not provide protection from typhoons, sun, and...
TABLE 5. Mean ± SE of slope (degrees), DBH (cm), and number of stems (counts) discriminating the six study sites for nesting Mariana Crows.

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>Mean DBH</th>
<th>Mean # Stems</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. marianensis</td>
<td>5.25 ± 0.36</td>
<td>15.87 ± 0.36</td>
<td>3.95 ± 0.43</td>
</tr>
<tr>
<td>A. coryacea</td>
<td>7.69 ± 0.69</td>
<td>19.39 ± 0.69</td>
<td>3.14 ± 0.24</td>
</tr>
<tr>
<td>C. fulvicincta</td>
<td>7.13 ± 0.71</td>
<td>19.13 ± 0.71</td>
<td>2.00 ± 0.20</td>
</tr>
<tr>
<td>D. magna</td>
<td>6.44 ± 0.65</td>
<td>20.64 ± 0.65</td>
<td>3.25 ± 0.25</td>
</tr>
<tr>
<td>E. crassipes</td>
<td>6.06 ± 0.61</td>
<td>21.66 ± 0.61</td>
<td>3.14 ± 0.21</td>
</tr>
<tr>
<td>O. m. mariamensis</td>
<td>6.06 ± 0.61</td>
<td>21.66 ± 0.61</td>
<td>3.14 ± 0.21</td>
</tr>
</tbody>
</table>

The understory may be too sparse to provide the vegetative complexity for successful foraging if the forest is too mature. Similarly, the Florida Scrub-Jay has been shown to favor scrub oak (*Quercus dumosa*) in 80% of its nest substrate (Bowman and Woolfenden 2002).

A limitation of our work is that the six study plots were not originally chosen to be representative of the forest on Rota. They represented contiguous crow habitat and were considered for special habitat protection by the U.S. Fish and Wildlife Service (Morton et al. 1999). Thus, they represent a range of Mariana Crow densities ranging from 3 to 9 pairs per site, or an average of one pair/22 ha (Morton et al. 1999). We believe the sites are representative of Mariana Crow nesting habitat. There were significant differences in vegetation between study sites (Table 5), but only one species associated with successful nests varied between sites (Lipstick tree, *Ochrosia mariamensis*). This tree species is known to have been used for nesting by Mariana Crows on Rota, but is rarely used (Morton et al. 1999). Island-wide comparison of nest site selection and habitat use by Mariana Crows, as well as a nesting tree species and territory tenacity analysis, and ongoing efforts to film nest activity may reveal micro-differences in habitat resources that affect reproductive success in these endangered birds.

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Woolfenden 2002; J. C. Ha, unpubl. data) or mobbing by Black Drongos (*Dicrurus macrocerus*) or Micronesian Starlings (*Aplonis opaca*).
Service (Endangered Species, Section 6). All research was conducted under Federal Endangered Species Permit FWSPIO-3, Federal Bird Marking and Salvage Permit 22570, and an amended CNMI Fish and Game Permit 068-95-SPN.

LITERATURE CITED


ABSTRACT.—Aspects of the breeding biology of the world largest Olrog’s Gull (Larus atlanticus) colony, in the estuary of Bahía Blanca, Argentina, were assessed for 101, 66, and 47 nests in 2005, 2006, and 2007, respectively. Mean (± SD) clutch size in 2005 was 1.86 ± 0.73 eggs per nest and modal clutch size was two eggs (range = 1–3). The incubation period was 1.67 days longer for A-eggs than for B-eggs (27.44 ± 1.22 days vs. 25.77 ± 1.36 days, respectively; P < 0.001). Incubation length for C-eggs was 25.75 ± 0.96 days. The largest eggs were 31.5% (length), 21.3% (breadth), and 66.5% (volume) larger than the smallest eggs. Mean egg volume in 2006 and 2007 decreased with hatching order, but the magnitude of this change was more pronounced in 2007 than in 2006. Variation in all egg measurements was larger among than within clutches. Hatching success within three-egg clutches was 76.9% in 2005, 81.7% in 2006, and 91.3% in 2007 (P = 0.20). Total egg loss in 2005 reached 16.7% and complete clutch loss was 43.8% during the incubation period. Parameters quantified in this study provide a comparative benchmark for future research on factors affecting breeding parameters in Olrog’s Gull from this and other colonies, and lay the foundation for developing effective conservation strategies for the species.

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clutch size. New eggs observed in each nest were marked with non-toxic indelible ink to indicate first, second, and third-laid eggs, and denoted as A-, B-, and C-eggs. The colony was left undisturbed during incubation of the study clutches (8-27 Oct 2005). A different methodology for nest selection was used in 2006 and 2007 due to the logistical constraints of the area. Study nests with 1-3 eggs were selected in 2006 (n = 66) and 2007 (n = 47) during late incubation (16 Oct-9 Nov 2006, 4-17 Oct 2007) based on observations that suggested imminent hatching of at least one egg, such as small cracks in the shell or a star-pipped egg. Sampling in 2006 was conducted after hatching had begun, and 14 days later in the season than in 2007. Nest selection in the second year started at onset of hatching. Eggs were marked based on signs of hatching to indicate presumed first, second, and third hatching order, and denoted as A-, B-, and C-eggs. Only nests near the periphery were selected in 2006 and 2007 to minimize disturbance in the inner areas of the colony. Each egg was measured (max breadth and length, nearest 0.01 mm) using digital calipers (Mitutoyo, Kawasaki, Japan). Egg volume (V) was calculated in cm$^3$ as $V = 0.000476 \times \text{length} \times \text{breadth}^2$ (Bolton 1991).

Nests were visited daily during the hatching period of the marked clutches (27 Oct-2 Nov 2005, 17 Oct-9 Nov 2006, 4-24 Oct 2007) to: (1) ascertain hatching date, (2) estimate incubation length (only in 2005), (3) identify hatching order, (4) examine extent of hatching asynchrony, and (5) calculate hatching and breeding success. Incubation length for individual eggs in 2005 was defined as the time elapsed between laying and hatching date of the same egg. Laying date was defined as the date a new egg was first observed in the nest. Synchronous hatching was defined as hatching of two eggs within the same 24-hr period and producing chicks without overt physical or behavioral differences. Hatching success was defined as the proportion of marked eggs that hatched successfully in three-egg clutches, and breeding success was the number of chicks produced per nest in three-egg clutches. Eggs in all years were considered lost or depredated if not found after the initial visit, or if found broken. Eggs which did not show signs of hatching 6 days after hatching of the last egg in the clutch were considered hatching failures.

**Statistical Analyses.**—The exact laying dates could not be ascertained in 2005 (nest visits every second day), and differences in incubation period between egg-types should be interpreted with caution. Study nests in 2006 and 2007 were selected upon hatching of the first egg in the clutch, and length of incubation could not be calculated. Hatching success was calculated in all three seasons but breeding success was calculated only in 2006 and 2007 because of our failure to monitor all eggs within clutches in 2005. The observed clutch size upon nest selection in 2006 and 2007 may have been different from the original size at the end of laying due to egg loss and predation. Considering this potential source of bias, hatching and breeding success in any year were calculated using only three-egg clutches, and hatching intervals between eggs from the same nest were not calculated in two-egg clutches from 2006 and 2007.

Data from eggs measured in three-egg clutches in 2006 and 2007 (151 eggs from 55 clutches) were used for a general description of egg size and to investigate egg size variation within and among clutches. Egg volume is a composite of egg breadth and length, and it was used in the investigation of factors affecting egg size in three-egg clutches. Generalized linear mixed models (GLMM) were built using the function “lmer” in the “lme4” package (Bates and Maechler 2009) of R (R Development Core Team 2009). Variables investigated were “hatching order” (first, second, third), “year” (2006, 2007), and their two-way interaction. Nest identification number (NEST ID) was included as a random effect to account for correlated variation among eggs in the same nest (Pinheiro and Bates 2000). Model building was based on maximum likelihood (ML) and the final model was fitted by restricted maximum likelihood estimation (REML) (Zuur et al. 2009). $P$-values were calculated by Markov Chain Monte Carlo simulations in R using the “coda” package (Plummer et al. 2009) due to unresolved issues regarding estimation of the degrees of freedom associated with fixed effect coefficients in mixed models (Bates 2006). The significance of the models was assessed using Akaike’s Information Criterion (AIC; Akaike 1974). Variables were removed unless they reduced the AIC by more than two units when included (Burnham and Anderson 2002).

Source of variation in egg measurements (breadth, length, and volume within and among clutches) was estimated by variance component
TABLE 1. Incubation period (days) (mean ± SD) for Olrog’s Gulls in the 2005 breeding season at Isla del Puerto, Argentina breeding colony. Data stratified by laying order and clutch size.

<table>
<thead>
<tr>
<th>Laying order</th>
<th>One-egg</th>
<th>Two-eggs</th>
<th>Three-eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-eggs</td>
<td>28.00 ± 2.83 (26–30, n = 2)</td>
<td>27.26 ± 1.10 (25–29, n = 19)</td>
<td>27.64 ± 1.21 (25–29, n = 11)</td>
</tr>
<tr>
<td>B-eggs</td>
<td>NA</td>
<td>25.70 ± 1.03 (24–27, n = 20)</td>
<td>26.00 ± 2.00 (24–29, n = 29)</td>
</tr>
<tr>
<td>C-eggs</td>
<td>NA</td>
<td>NA</td>
<td>25.75 ± 0.96 (25–27, n = 4)</td>
</tr>
</tbody>
</table>

NA = Not applicable.

models (Crawley 2007) using the same approach described above, except that NEST ID was the only variable evaluated (as random effect) and no independent variables were included in the models. Repeatability of each egg measurement (i.e., the proportion of variance in a character that occurs among rather than within individuals; Boag and van Noorwijk 1987) was estimated from the variance component models.

The size of difference in volume among A-, B-, and C-eggs from three-egg clutches in each year was calculated using Cohen’s d value as effect size statistic (Nakagawa 2004). Effect size was expressed as percentage using the Common Language Effect Size Statistic (CL) (McGraw and Wong 1992) for easier interpretation. For example, a CL of 64.4 between B- and C-eggs indicates the probability that a randomly selected B-egg will be larger than a randomly selected C-egg is 64.4%.

Differences in hatching success among years and differences in hatching success among different clutch sizes (only in 2005) within three-egg clutches were assessed using Chi-square tests for trend. Differences in total clutch volume in three-egg clutches between 2006 and 2007, and in length of incubation between A- and B-eggs regardless of clutch size (only in 2005), were assessed using unpaired t-tests. Level of significance was defined as P < 0.05. Descriptive statistics are presented as means ± SD, and medians and ranges are reported where appropriate. Residual and normal probability plots were used to check for validity of model assumptions.

RESULTS

Laying and Incubation.—Egg laying in 2005 began during the first week of September and followed an asynchronous pattern. Mean ± SD clutch size was 1.86 ± 0.73 eggs per nest (n = 101 clutches) and modal clutch size was two eggs (range = 1–3). Data for incubation periods varied (Table 1). The incubation length (all clutch sizes considered) for A-eggs in 2005 was 1.67 days longer than for B-eggs (27.44 ± 1.22 days vs. 25.77 ± 1.36 days, respectively; unpaired t-test: df = 60, P < 0.001), and incubation for C-eggs was 25.75 ± 0.96 days (n = 4).

Egg Dimensions and Size Variation.—We measured 253 eggs from 113 one-, two-, and three-egg clutches during the 2006 and 2007 breeding seasons (Table 3). Large ranges in egg size were detected with the largest eggs being 31.5% (length), 21.3% (breadth), and 66.5% (volume) larger than the smallest. Egg length

---

TABLE 2. Generalized linear mixed model describing factors associated with egg volume of Olrog’s Gulls during the 2006 and 2007 breeding seasons at Isla del Puerto, Argentina breeding colony.

<table>
<thead>
<tr>
<th>Terms</th>
<th>Coefficients</th>
<th>SE</th>
<th>P</th>
<th>Δ AIC*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>79.4672</td>
<td>1.1766</td>
<td>&lt;0.001</td>
<td>NA</td>
</tr>
<tr>
<td>Hatching order (Ref.: First)</td>
<td>-0.1122</td>
<td>0.8058</td>
<td>0.89</td>
<td>8.0</td>
</tr>
<tr>
<td>Hatching order (Third)</td>
<td>0.2075</td>
<td>0.8066</td>
<td>&lt;0.001</td>
<td>NA</td>
</tr>
<tr>
<td>Year (Ref.: 2006)</td>
<td>-4.0287</td>
<td>1.6375</td>
<td>0.015</td>
<td>NA</td>
</tr>
<tr>
<td>Hatching order (Second)*2007</td>
<td>-3.2167</td>
<td>1.1563</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td>Hatching order (Third)*2007</td>
<td>-4.2275</td>
<td>1.1604</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

* AIC value increment if the single term is dropped.
TABLE 3. Olrog’s Gull egg measurements. Length (mm), maximum breadth (mm), and volume (cm$^3$) are reported for each egg type in three-egg clutches from 2006 and 2007 at Isla del Puerto, Argentina breeding colony. Measurements are mean ± SD. Sample size in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Hatching order</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A-egg</td>
<td>B-egg</td>
<td>C-egg</td>
</tr>
<tr>
<td>2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>69.96 ± 3.36 (26)</td>
<td>69.28 ± 2.96 (25)</td>
<td>69.07 ± 2.60 (24)</td>
</tr>
<tr>
<td>Breadth</td>
<td>48.80 ± 1.68 (26)</td>
<td>49.03 ± 1.58 (25)</td>
<td>48.01 ± 1.63 (24)</td>
</tr>
<tr>
<td>Volume</td>
<td>79.44 ± 7.04 (26)</td>
<td>79.44 ± 7.11 (25)</td>
<td>75.90 ± 6.15 (24)</td>
</tr>
<tr>
<td>2007</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>73.32 ± 2.53 (24)</td>
<td>70.17 ± 3.01 (23)</td>
<td>69.23 ± 2.69 (23)</td>
</tr>
<tr>
<td>Breadth</td>
<td>49.02 ± 0.91 (24)</td>
<td>49.12 ± 1.17 (23)</td>
<td>47.94 ± 1.28 (29)</td>
</tr>
<tr>
<td>Volume</td>
<td>83.90 ± 4.28 (24)</td>
<td>80.63 ± 5.33 (23)</td>
<td>75.80 ± 5.38 (29)</td>
</tr>
</tbody>
</table>

The results of the final model assessing the variables that best explained variation in egg volume varied (Table 2). Mean egg volume decreased with hatching order in three-egg clutches in 2006 and 2007. The magnitude of this change was significant in both years, and was more pronounced in 2007 (Fig. 2). B- and C-eggs in 2006 were 0.11 and 3.50 cm$^3$ smaller, respectively, than A-eggs, and C-eggs were 3.39 cm$^3$ smaller than B-eggs. B- and C-eggs in 2007 were 3.33 and 7.73 cm$^3$ smaller respectively, than A-eggs, and C-eggs were 4.40 cm$^3$ smaller than B-eggs (Fig. 2).

The variance component models for egg size revealed variation in all egg measurements was larger among than within clutches. Egg length varied 56.8% among clutches and 43.2% within clutches, egg breadth varied 65.9% among clutches and 34.1% within clutches, and egg volume varied 61.5% among clutches and 38.5% within clutches.

Hatching.—Hatching began on 5 October in 2005 and during the last week of September in 2007. The date of hatching onset could not be ascertained in 2006, because we arrived at the colony after hatching began. Eggs hatched asynchronously in the order they were laid in 2005 (Spearman $r = 0.835$, 95% CI: 0.77–0.91, $P > 0.001$) with the exception of a few eggs (5 pairs of A-B eggs and 1 pair of B-C eggs) which hatched synchronously despite having been laid days apart. Similarly, hatching in 2006 and 2007 was asynchronous in most clutches with a few eggs (2006: 5 pairs of A-B eggs; 2007: 5 pairs of A-B eggs) hatching synchronously. Hatching intervals between eggs varied (Table 4).

Hatching success in three-egg clutches was 76.9% (30/39) in 2005, 81.7% (58/71) in 2006, and 91.3% (63/69) in 2007 ($\chi^2$ for trend = 6.00, df = 4, $P = 0.20$). Breeding success was 2.42 chicks per nest in 2006, and 2.74 chicks per nest in 2007. Hatching and breeding success were likely overestimated in 2006 and 2007 due to our method of nest selection. Breeding success could not be ascertained in 2005 due to the low sample size of three-egg clutches in which all eggs could be monitored. Hatching success in 2005 was not different among different clutch-sizes (1 egg: 68.4%; 2 eggs: 75.4%; 3 eggs: 76.9%; $\chi^2$ for trend = 6.00, df = 4, $P = 0.20$). Total egg loss and complete clutch loss in 2005 in the colony was similar among different clutch sizes (Table 5).

**DISCUSSION**

Quantifying the reproductive biology of species of conservation concern is vital for developing effective conservation strategies. Despite the existence of additional, albeit smaller reproducing colonies of Olrog’s Gull, comparative information from those colonies is not available. Therefore, our findings cannot be completely correlated with existing research on this species.

**Laying, Incubation, and Hatching.—** The modal clutch size of two eggs in 2005 agrees with reports...
FIG. 1. Distribution of egg volume for different egg types in three-egg clutches, and total clutch volume for Olrog's Gull, Isla del Puerto, Argentina breeding colony. The middle 50% of the data (box), 25th and 75th percentiles (lower and upper hinges), median (line), mean (cross) and minimum and maximum (whiskers) are displayed by year. P-values show statistical difference between years.

FIG. 2. Volume of Olrog's Gull eggs at Isla del Puerto, Argentina breeding colony in 2006 and 2007. The effect of hatching order on egg volume was significant in both years and depended on the year of sampling, being more pronounced in 2007. Numbers (%) represent effect size statistic (CL) comparing egg volume between egg types sampled in 2006 (below the line) and 2007 (above the line), and indicate the probability that an egg randomly selected from the category on the left of CL will be larger than a randomly sampled egg from the category on the right in the same year.

by other authors for some gull species (Beer 1966, Yorio et al. 1996), but does not correspond with the modal clutch size of three eggs most commonly reported in gulls (Lack 1968, Winkler and Walters 1983, Reid 1987). Selection of study nests in 2005 was based on the presence of one egg (A-egg) and were visited every second day, which precluded accurately estimating clutch initiation dates and incubation periods in that year. Thus, the length of incubation for A-eggs was likely underestimated while that for B- and C-eggs may have been overestimated by a maximum of 48 hrs.

Hatching asynchrony in all seasons led to broods with hatching-order-dependent age hierarchy among siblings, as has been reported for other species of gulls (Graves et al. 1984, Pierotti and Bellrose 1986, Sydeman and Emslie 1992, Royle and Hamer 1998). Synchronous hatching of some eggs in all seasons may be more a reflection of our daily nest visit schedule, which affected our ability to detect exact hatching times. It is also
TABLE 4. Hatching intervals (days) of two and three-egg clutches in 2005 and three-egg clutches in 2006 and 2007 at Isla del Puerto, Argentina breeding colony. Values are mean ± SD with range in parentheses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Clutch Size</th>
<th>Hatching interval (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A/B</td>
</tr>
<tr>
<td>2005</td>
<td>Two eggs</td>
<td>0.91 ± 0.83 (0–2) (n = 11)</td>
</tr>
<tr>
<td></td>
<td>Three eggs</td>
<td>0.83 ± 0.75 (0–2) (n = 6)</td>
</tr>
<tr>
<td>2006</td>
<td>Three eggs</td>
<td>1.42 ± 0.77 (0–3) (n = 19)</td>
</tr>
<tr>
<td>2007</td>
<td>Three eggs</td>
<td>1.12 ± 0.65 (0–4) (n = 19)</td>
</tr>
</tbody>
</table>

NA = Not applicable.

possible that pairs whose clutches were laid over several days but hatched synchronously, began incubation upon laying of the second egg and not immediately after the first egg was laid, delaying embryo development and eliciting some A- and B-eggs to hatch synchronously.

The level of egg mortality (16.7%) and complete clutch loss (43.8%) reported during the incubation period in the study colony could have conservation implications through depressed breeding success for a vulnerable species. Spring tidal floodings are relatively common in the estuary of Bahía Blanca (Capelli and Campo 2004) and can severely affect hatching and reproductive success of Olrog’s Gull by soaking or washing away eggs and chicks (L. F. La Sala, unpubl. data). However, no tidal flooding or extreme weather conditions were reported during incubation in 2005 suggesting predation of unattended eggs may have been substantial in the study colony. This assumption is supported by a recent report of predation of Olrog’s Gull chicks by adult Kelp Gulls (La Sala and Martorelli 2010) accompanied by a sustained growth of the Kelp Gull colony surrounding the studied Olrog’s Gull colony (P. F. Petracic, unpubl. data). The colony was left undisturbed in 2005 after nest selection and throughout the incubation period, but we cannot rule out investigator impact as a possible cause of some nest abandonment (Fetterlof 1983) or interspecific aggression and predation.

The proportion of eggs hatched and young fledged often differ markedly in relation to nest location in colonies of many bird species. Some studies report gulls nesting in the central part of a colony hatch proportionately more eggs and raise more young than birds with nests on the periphery (e.g., Dexheimer and Southern 1974), but other authors failed to find such differences (Ryder and Ryder 1981). The spatial distribution of selected nests in our study (peripheral and central in 2005, and only peripheral in 2006 and 2007) represents a potential source of bias; thus, our results of hatching success among years should be interpreted with caution.

Within and Between-clutch Egg Size Variation.—Repeatability of egg size may be used to set an upper limit to the value of heritability, in addition to its use in assessing the reliability of multiple measurements of the same individual (Falconer 1981). Egg size varies greatly within many avian species with the largest eggs in a given population generally being at least 50%
Mills (1979) reported egg size variation between hatch/fledge a greater proportion of their eggs and many species (Christians 2002). Previous work has contributed to the inter-annual variation lands has shown that older birds lay larger Individual females, and increases slightly with age the volume of B- and C-eggs does not seem to larger A-eggs in 2007 compared with 2006. While however, would be attributable to considerably more pronounced in 2007. This difference, strongly on the year of sampling, being much 007. The intensity of this trend depended along the hatching sequence both in 2006 and 2007. The intensity of this trend depended strongly on the year of sampling, being much more pronounced in 2007. This difference, however, would be attributable to considerably larger A-eggs in 2007 compared with 2006, while the volume of B- and C-eggs does not seem to have contributed to the inter-annual variation observed.

Egg size appears to be a characteristic of individual females, and increases slightly with age in many species (Christians 2002). Previous work with larids has shown that older birds lay larger clutches, initiate breeding earlier each season, and hatch/fledge a greater proportion of their eggs and chicks (Pyle et al. 1991, Sydeman et al. 1991). Mills (1979) reported egg size variation between seasons and presented evidence that the most efficient foragers and older females produce the largest eggs.

There are no studies of the breeding phenology of Olrog’s Gull in the estuary of Bahía Blanca. Long-term monitoring would be necessary to understand inter-annual variations in egg size, but it is possible that in 2006 we sampled a greater proportion of nests of late and younger breeders which laid smaller eggs and, most notably, smaller A-eggs compared with 2007. Following this hypothesis, the smaller volume of three-egg clutches from 2006 would have been produced by younger, less experienced females.

ACKNOWLEDGMENTS

The authors especially thank Club Náutico Bahía Blanca, Nicolás Acosta, Joaquín Ceregueti, Martín Sotelo, Lucía Díaz, and the Fernandez family for their unwavering support. We thank the anonymous reviewers whose suggestions resulted in substantial improvements to this article. This study was partly funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT 3442/05).

LITERATURE CITED


BIPARENTAL CARE AND NESTING SUCCESS OF THE SWALLOW-TAILED COTINGA IN NORTHWESTERN BOLIVIA

VERÓNICA DEL ROSARIO AVALOS

ABSTRACT.—I studied the breeding biology, parental care, and nesting success of the Bolivian Swallow-tailed Cotinga (Pinhalura flavirostris boliviana) in Aten, northwestern Bolivia, from October 2005 to February 2006. The incubation period ranged from 17 to 19 days and the nestling period was 25 to 30 days. Swallow-tailed Cotingas appeared to be monogamous during the entire nesting stage, from nest construction to fledging of nestlings, based on 10 nests with focal observations. Each parent took care of the nest every hour during the incubation period, but males spent more time at this activity than females. Both parents spent equal time taking care of the young during the nestling period. Nest care decreased as nestlings developed, the provisioning rate of parents increased, and length of foraging trips increased. The probability of daily survival between the nestling (0.9773) and incubation periods (0.9455) was not statistically significant; overall nesting success was low (20%). This work is the first detailed report of the nesting of this species in Bolivia.

Breeding biology has been a principal concern in ecological studies of birds because this information is important to understanding life histories, including social and reproductive systems, population dynamics, and biological conservation (Stutchbury and Morton 2001, Green 2004). Among mating systems, monogamy is most common in birds, even in the tropics (Gill 1995, Stutchbury and Morton 2001). In this system, birds form a prolonged and essentially exclusive pair bond for purposes of raising young (Gill 1995, Cockburn 2006). Both parents construct the nest, incubate the eggs, and feed the nestlings. The extent of parental participation in each activity varies by species and length of the nesting period, which reflects growth of nestlings (Gill 1995).

In contrast, lek displays of polygynous birds are more characteristic of cotingas. Females visit males only for purposes of fertilization and care for their young by themselves (Snow 2004). For some cotingas, such as fruiteaters (Pipreola spp.), purplefrills (Iolepleura spp.), and the Black-faced Cotinga (Conioptilon mehelyi), monogamy and biparental care prevail (Snow 2004). However, few quantitative studies of parental care by cotingas exist (but see Amaya-Espinell 1997, Kambian et al. 2003). Nesting success of most cotingas is unknown because their nests are cryptic and difficult to locate and observe (Snow 2004). Studies have shown that nesting success of the Guianan Cock-of-the-rock (Rupicola rupicola) and Bearded Bellbird (Procnias averano) are low because of unfavorable climatic factors and predation (Snow 2004). It is also low for the Andean Cock-of-the-rock (R. peruvianus) because of habitat modification and human activities (Sarria-Salas 2005). Nesting success is reportedly low in neotropical birds in general (Skutch 1985, Martin 1996), but more research is needed.

The near-threatened (IUCN 2008) Swallow-tailed Cotinga (Pinhalura flavirostris) is also a poorly known species, and observations of its nesting behavior are limited (Snow 2004) despite nesting in open areas. The nests and eggs of Pinhalura f. flavirostris (Fraga and Narosky 1985) and Pinhalura f. boliviana (Bromfield et al. 2004) have been described, but little is known about incubation of this species. Both males and females appear to care for nestlings although quantitative information on parental care is lacking (Snow 1982, Ridgely and Tudor 1994, Snow 2004). Only a single population of Pinhalura f. boliviana is known from Bolivia, and it may be specifically distinct from the Brazilian populations. Information on the breeding biology of this species could contribute to its conservation and to our ability to manage it. I present basic data on incubation and nestling care of the Bolivian Swallow-tailed Cotinga (Pinhalura f. boliviana). I also report parental investment in both activities, and nesting success.

METHODS

Study Area.—I conducted this study in the locality of Aten (68° 19' W, 14° 55' S; 1,400–
1,690 m asl), in the central eastern Andes south of Apolo, La Paz Department, Bolivia. The area contains semi-humid forest fragments, montane savannas, and farm pastures. The forest fragments are drier than wet forests and have fewer species (Foster and Gentry 1991). Local farmers frequently burn the montane savannas and farm pastures (Miranda 2005). Consequently, the vegetation consists of a thin cover of grass and other forbs mixed with gnarled shrubs and small tress including *Alchornea* spp. (Euphorbiaceae) (Foster and Gentry 1991) with dominant *Schefflera morototoni* trees (Araliaceae) scattered throughout the study area. The wet season normally occurs from October to March, and it is dry between April and August. Average annual temperatures range from 16 to 20°C; October is the hottest month with temperatures reaching a maximum of 28°C (SENAMHI 2006).

Nest Monitoring.—I found active nests by intensively searching (following Martin and Geupel 1993) in montane savanna habitat from late October 2005 to early March 2006. I monitored nests every 2–4 days to ascertain length of nesting periods and nesting success. The incubation period was calculated as the number of days between laying of the last egg and hatching of that egg (Gill 1995). The nesting period was considered the number of days between hatching of the last egg and fledging of the last nestling. Nests found in the building process were followed until completion.

I observed parental care of birds at nests at 1 to 4 day intervals, either from 0630–1200 or 1400–1830 hrs from a distance of 20 m using 10 X 45 binoculars. Adults did not appear to be bothered by my presence at this distance.

I collected incubation period data at five nests, distinguishing three types of parental behavior: incubation, perching in trees in the nesting area, and absence from the nesting area. I collected data from an additional five nests during the nesting period distinguishing the following types of parental behavior: (1) total attendance that included parental care at the nest and parental care at the nest from a distant tree perch (vigilance), (2) parental provisioning of nestlings, and (3) foraging trips. Parental care at the nest consisted of brooding nestlings or perching near the nest (~5–50 cm). Parental care from a distant tree perch consisted of perching in trees (including the nest tree) within a 10-m radius of the nests, which occurred each time a parent arrived with a food item or provisioned nestlings. I recorded the number of visits and the rate at which parents provisioned nestlings (food item/hr/parent). I recorded each "foraging trip" as the length of time a parent was absent from the nesting area. Observation of nests allowed me to distinguish nestling's traits by their age.

I estimated nesting success for the incubation and the nesting periods separately and combined. Nest success was defined as at least one egg hatching, and nesting success as at least one young fledging (Gill 1995). I observed parental activities, checked the contents of nests, and searched for fledglings in the nesting area to verify nesting activity (Green 2004). I considered nests to be (1) active, if parents displayed nearby activity, or if individuals were seen within the nest; (2) predated, if there was sign of predation such as eggshell fragments, nest material scattered around the area, or nestlings had disappeared prior to the time of potential fledging; (3) deserted, if the parents did not attend or stopped attending the nest; and (4) other, if climatic conditions or location of nest influenced nesting success.

Statistical Analyses.—Average time (min/hr) that each parent spent incubating, providing parental care at the nest, providing parental care from a tree perch, and provisioning rates as well as foraging trips was compared using a paired t-test. Repeated measure ANOVA tests were used to analyze six nestling-age categories based on extent of feather development and nestling size: 1 = 2–5 days, 2 = 6–9 days, 3 = 10–13 days, 4 = 14–17 days, 5 = 18–22 days, and 6 = 23–27 days. Post-hoc tests were conducted for repeated measures with Bonferroni corrections if differences were significant.

I checked normal distribution of the data using Kolmogorov–Smirnov tests, and data homogeneity using the F-max test. The compound symmetry assumption was verified with Huynh-Feldt epsilon approaches when repeated measures ANOVAs were needed. A Wilcoxon test was used for comparing differences between males and females, and a Friedman test was used for comparing age categories if data violated these assumptions. Statistical analyses were conducted using SYSTAT 11.0 (2004) at the significance level of α = 0.05.

The daily probability of survival was calculated following Mayfield (1961, 1975). This estimate results from the total number of days when nests are active (exposure days) divided by the number
TABLE 1. Duration of parental care of eggs (min/bout) by male and female Bolivian Swallow-tailed Cotingas (Phibalura f. boliviana) at five nests. Values = mean ± SD.

<table>
<thead>
<tr>
<th>Categories</th>
<th>Nest number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total hours observed</td>
<td>24.5</td>
<td>19.3</td>
<td>19.3</td>
<td>35.5</td>
</tr>
<tr>
<td>Incubation time</td>
<td>Male</td>
<td>49.8 ± 54.4</td>
<td>57.1 ± 34.0</td>
<td>119.3 ± 56.1</td>
<td>98.4 ± 74.9</td>
<td>80.3 ± 39.5</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>35.7 ± 28.8</td>
<td>48.5 ± 22.3</td>
<td>39.3 ± 27.9</td>
<td>72.5 ± 52.7</td>
<td>51.7 ± 27.0</td>
</tr>
<tr>
<td>Perching time</td>
<td>Male</td>
<td>7.5 ± 7.7</td>
<td>36.5 ± 30.4</td>
<td>10.0 ± 7.1</td>
<td>20.0 ± 9.8</td>
<td></td>
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<tr>
<td></td>
<td>Female</td>
<td>3.5 ± 2.1</td>
<td>14.0 ± 5.6</td>
<td>1.8 ± 0.8</td>
<td>5.0 ± 4.2</td>
<td></td>
</tr>
<tr>
<td>Unattended eggs</td>
<td></td>
<td>10.8 ± 7.2</td>
<td>14.0 ± 7.9</td>
<td>28.0 ± 18.3</td>
<td></td>
<td>10.0 ± 5.2</td>
</tr>
</tbody>
</table>

RESULTS

Nesting.—The first nest was found on 8 November 2005 and contained one ~13 day-old nestling. The last nest was discovered on 4 March 2006 and contained one ~10 day-old nestling. Both parents constructed nests using lichens and thin twigs collected from trees with few leaves (e.g., Alchornea triplinervia). Both parents emitted smooth guttural whistles with descending notes during the nest-building process. Nests for which construction was ~20% complete required 5.3 ± 0.8 days (range = 4–6, n = 5) to build. The clutch size of Phibalura f. boliviana was two eggs, laid on 2 consecutive days (n = 7). The incubation period was 18 ± 0.8 days (range = 17–19 days, n = 6) and the nestling period was 27 ± 1.7 days (range = 25–30 days, n = 9). The earliest age that a nestling left the nest was on day 23, after being disturbed by cattle.

Parental Care.—Both parents incubated the eggs (92% of the time) with interchange every hour on average (Table 1). However, parents also spent time defending their territory from other mated pairs in the early stages of incubation, and perching in trees near the nest site (Table 1). The mean duration of incubation for males was significantly longer than for females (males: 30.1 ± 12.4 min/hr; females: 20.7 ± 10.3 min/hr; paired t-test = 2.2, df = 22, P = 0.037). Time spent perching in trees did not differ significantly between males and females (paired t-test = 1.0, df = 13, P = 0.328).

Parents allocated their time during the nestling period to different care-related activities (Fig. 1, Table 2). Parents initially provided almost continuous care for small nestlings (99% of time), brooding with a rate of interchange of 12 to 27 min (Table 2) and showing an alert position when it was time to feed them. However, total attendance by parents at a nest (parental care at both the nest and from a distant tree perch) declined as age of nestlings increased (Fig. 1). Mean brooding time decreased with nestling age (F = 14.5, df = 4, 0.001).
TABLE 2. Duration of parental care of nestlings (min/bout) by male and female Bolivian Swallow-tailed Cotinga (Phibalura f. boliviana) at five nests. Values = mean ± SD.

<table>
<thead>
<tr>
<th>Categories</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6*</td>
</tr>
<tr>
<td>Total hours observed</td>
<td>69.6</td>
</tr>
<tr>
<td>Brooding time</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>18.6 ± 16.7</td>
</tr>
<tr>
<td>Female</td>
<td>18.5 ± 16.7</td>
</tr>
<tr>
<td>Perching time near nest</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>7.8 ± 8.4</td>
</tr>
<tr>
<td>Female</td>
<td>5.2 ± 5.4</td>
</tr>
<tr>
<td>Perching time in trees</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>4.7 ± 5.6</td>
</tr>
<tr>
<td>Female</td>
<td>5.2 ± 5.6</td>
</tr>
<tr>
<td>Foraging trip time</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>17.8 ± 10.7</td>
</tr>
<tr>
<td>Female</td>
<td></td>
</tr>
</tbody>
</table>

* Nest with fledglings.

\( P < 0.001, n = 5; \) Figs. 1-2), but was not significantly different between parents (paired \( t\)-test = 1.5, \( df = 24, P = 0.15; \) Table 2). Brooding time was lower for 18 to 22-day-old nestlings than for those 2 to 5 days of age (post-hoc test, \( P < 0.002; \) Figs. 1-2). The mean time that each parent spent brooding nestlings 18 to 22 days of age was 2.7 ± 2.0 min/hr versus 33.7 ± 17.1 min/hr for small nestlings (Fig. 2). Brooding ceased at 22 days (Fig. 1), except during adverse climatic conditions.

Brooding decreased once nestlings were 10 days of age and parents increased the time they spent perching near the nest. The mean amount of time parents spent perching near the nest increased by age categories (\( F = 11.2, df = 4, P < 0.001 \)). This behavior was higher for nestlings beginning at 18 days of age than at 10 days of age (post-hoc tests, \( P < 0.023 \)). Males perched near the nest longer than females (males: 8.8 ± 7.1 min/hr; females: 5.8 ± 7.9 min/hr; paired \( t\)-test = 2.264, \( df = 18, P = 0.036 \)). Parental care from a distant tree perch did not differ significantly between parents (\( Z = 1.5, P = 0.12 \), but varied with nestling age (Friedman test = 19.7, \( df = 4, P = 0.001 \)). Parents perched in trees when nestlings were small for 1.2 ± 0.9 min/hr and when the nestlings were older for 6.4 ± 8.6 min/hr.

Parental visits to the nest combined were at least twice per hour (2.4 ± 2.8 visits/hr, \( n = 5 \) nests). The provisioning rate to nestlings did not differ significantly between males and females (paired \( t\)-test = 0.4, \( df = 26, P = 0.67 \)), but did vary among age categories of nestlings (\( F = 18.8, df = 5, P < 0.001 \)). The provisioning rate by parent was higher for 14-day-old nestlings than for 2–5 day-old nestlings (post-hoc test, \( P < 0.03; \) Fig. 3). Males and females did not differ significantly in mean lengths of foraging trips (paired \( t\)-test = 3.4, \( df = 28, P = 0.074 \)), but varied among nestling age categories (\( F = 3.4, df = 5, P = 0.01 \)). Foraging trips were longer for 23–27 day-old nestlings than for those 18–22 days, and 2–5 days of age (\( P < 0.036 \)).

Nesting Success.—I located 48 active nests of Bolivian Swallow-tailed Cotinga in the vicinity of Aten. The probability of daily survival during incubation was 0.9455 (\( n = 44, \) total egg exposure days = 444, SD = 0.0045). The probability of daily survival during the nesting period was

![Mean time brooding (min)](image)
The probability of success during the incubation period was 36% (mean incubation period = 18 days) and 53% for the nestling period (mean nestling period = 27.5 days). The probability of daily survival during the nestling period was higher than during incubation period (X^2 = 16.18, df = 1, P < 0.001).

The probability of survival of a nest from incubation to fledging was 20%. Predation was the main cause of nest failure (72%). Eggs disappeared from 18 nests (75% of failures) and parents deserted six nests (25%) during the incubation period. Eight (72%), of 11 nests that failed during the nestling period, failed when nestlings were 18-20 days of age due to disappearance or the entire nest being destroyed. Three nests contained dead nestlings (28%) after heavy rain at night. I also found dead nestlings of 7 days of age on terrestrial bromeliads and rocks, apparently in failed attempts to fly from the nest. I did not observed predation directly, but I observed parental sentinel behaviors, including standing up in the nest, inclining the head and body, vocalizing alarm calls (especially females) in presence of tayras (*Eira barbara*), Squirrel Cuckoos (*Piaya cayana*), and while escaping from snakes.

**DISCUSSION**

The first nest of the Bolivian Swallow-tailed Cotinga that I discovered was in early November and contained older nestlings; the last nests were found in late February and early March 2006 and contained young nestlings. Bromfield et al. (2004) reported nests with eggs in late September in the Pata area (Apolo). These reports suggest the breeding season for the Bolivian Swallow-tailed Cotinga is from September to March, between the end of the dry season and the end of the wet season in the study area. This time of breeding might be related to food abundance (Stutchbury and Morton 2001). The length of the nesting period is consistent with records for medium-size cotingas (Snow 2004), and its variation in length among nests might be a result of external conditions including: climate, and proximity of cattle, local people, and predators that affect fledging of nestlings (Skutch 1945).

The clutch size for the Brazilian population (*Phibalura flavirostris*) is 2–3 eggs (Snow 2004). I recorded a clutch of two eggs for the Bolivian population in my study area, similar to fruiteaters in the Andes (Snow 2004). The eggs were incubated continuously and parents exchanged nest care every hour as in some other monogamous species (Monaghan and Nager 1997). However, incubation by both parents is unique among cotingas, even by those with biparental care (Snow 2004). Incubation periods of males were longer than those of females; probably because females needed more time to increase body mass after laying eggs.

Both parents spent equal amounts of time caring for the young during the nestling period, concordant with some tropical species with biparental care (Wheelwright 1983, Dyrcz 2000, Dobbs et al. 2001). Parental care decreased as nestlings grew, as is the case in multiple avian taxa (Gill 1995), including cotingas (Amaya-Espinell 1997, Quispe and Flores 2002, Karubian et al. 2003, Muir et al. 2008). Small nestlings at the beginning of the study were continuously brooded by the parents because they did not have feathers and were presumably incapable of thermoregulation (Gill 1995). Brooding decreased and parents increased the time they perched near the nest once feathers began to grow and nestlings were older.

Both parents perched in trees surrounding the nesting tree, which presumably facilitated predator observation (e.g., Breitwisch 1986, Hall and Karubian 1996, White et al. 2006). This was important because nestlings flapped and moved which may have drawn the attention of predators. Parents also seemed to avoid possible dangers when they: (1) waited in canopy trees carrying
fruits (e.g., Ocotea spp.) in their beak, (2) vocalized from a tree perch but did not meet simultaneously at the nest, and (3) perched in other trees when older nestlings vocalized constantly. Some of these behaviors have been observed in other birds (Breitwisch 1986, Hall and Karubian 1996, White et al. 2006), and served to diminish attraction of predators to the nest site.

I did not measure size of the food items carried by parents to the nestlings, because parents usually regurgitated directly to the young. However, the provisioning rate shows the relative parental effort, which was verified when the rate increased with nestling age. Both parents allocated equal and substantial provisioning to nestlings, which is different from frugivores and fruiteaters where principally males fed nestlings and only females brooded (Amaya-Espinell 1997, Gielis et al. 2006). Increased provisioning rates for older nestlings characterizes many tropical birds (e.g., Wheelwright 1983, Dyrcz 2000, Dobbs et al. 2001) including cotingas (Amaya-Espinell 1997, Willis and Oniki 1998, Karubian et al. 2003, Muir et al. 2008) and is elicited mostly by posture and nestling calls (Kilner and Johnstone 1997, Roulin et al. 2008) and is elicited mostly by posture and nestling calls (Kilner and Johnstone 1997, Roulin 2001). Conversely, brooding time which requires a lower energetic investment than provisioning young (Williams 1996), decreased. These behaviors illustrate the relation between growth of nestlings and parental investment.

My research confirms that nestling care by Bolivian Swallow-tailed Cotingas is biparental and the pair is monogamous. This differs from the behavior commonly found in the Cotingidae, where females care for nestlings (Snow 2004). These differences are presumably associated with frugivory or predation (Bechler and Foster 1988, Stutchbury and Morton 2001, Cockburn 2006). Willis and Oniki (1998) suggested high levels of predation in tropical closed forests might influence females to care for the nestlings by themselves. Nesting habitat may also influence monogamous behavior, as Bolivian Swallow-tailed Cotingas nest in open areas, which may have lower predation rates than closed forests (Skutch 1985).

Nesting success during incubation was lower than success during the nestling period. Mezquida and Marone (2001) suggested for other bird species that parents might defend nestlings more than eggs, or those nests under high predation pressure were likely of being destroyed by predators. Nests that survived at the nestling stage were those difficult for predators to locate. The nesting period was successful, but combined nesting success was low (20%), primarily because of predation (72%). Low nestling success and high nest predation appears to be common patterns among neotropical birds (Martin et al. 2000, Stutchbury and Morton 2001), especially among understory birds (Robinson et al. 2000) and Cotinga species (Snow 2004). The high number and diversity of nest predators in the Neotropics may have resulted in this pattern (Stutchbury and Morton 2001). Tayras, birds of prey, cuckoos, snakes, rodents, and weasels are nest predators (Skutch 1985, Roper and Goldstein 1997, Eisenberg and Redford 1999, Dobbs et al. 2001, Patrick et al. 2004, Auer et al. 2007) that occur in savanna habitat and forest fragments. Predators may have also increased because of habitat modification (Martin 1996). More detailed studies of predation during the nestling period of Bolivian Swallow-tailed Cotingas are needed. Climate may also influence nesting success of birds (Robinson et al. 2000) and less concealed nests of the cotingas failed after heavy rains; long-term studies may be useful for evaluating the influence of climate, and climate change on the population. Increased rain or adverse weather conditions might influence the success rate of the species. This work provides the first behavioral and ecological information on nesting of the Bolivian Swallow-tailed Cotinga and can serve as a baseline for future research on nesting success in this species and its conservation.

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LITERATURE CITED


Avalos • REPRODUCTION OF SWALLOW-TAILED COTINGA

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Territorial, Parque Nacional Natural Farallones de Cali, Cali, Colombia.


VARIATION IN BREEDING OF THE SHRIKE-LIKE TANAGER IN CENTRAL BRAZIL

CHARLES DUCA*1,3,4 AND MIGUEL Â. MARINI2

ABSTRACT.—The Shrike-like Tanager (Neothraupis fasciata) is a Cerrado bird considered as near threatened. Its life history is poorly known, especially its reproduction. We monitored reproduction during four breeding seasons (2003–2006) with 120 nests in a protected area in central Brazil. Nesting began at the end of the dry season and start of the rainy season. The incubation (13.0 days) and nestling (11.7 days) periods were shorter than for most neotropical birds, but similar to some other tanagers. Clutch size (2–3 eggs) was similar to most tropical birds. However, clutch size increased and nest initiation date advanced ~30 days in a year of early precipitation compared to 3 other years with regular or late precipitation. The Shrike-like Tanager had breeding flexibility and ability to adapt to changes in temporal precipitation patterns. Received 23 July 2010. Accepted 21 December 2010.

Understanding population dynamics is of fundamental importance in ecology, evolution, and conservation, especially in regions with habitat loss or other anthropogenic degradation. The Shrike-like Tanager (Neothraupis fasciata), the only species in this genus, occurs in the Cerrado (neotropical savanna) and is classified as near threatened (IUCN 2009). It is a generalist forager (Alves 1991) occurring at altitudes from 500 to 1,100 m (Ridgely and Tudor 1994). It constructs a basket-shaped nest <1 m above ground (Alves and Cavalcanti 1990) and often is a sentinel in mixed species flocks (Alves 1990, Raguazi-Neto 2000). It is monogamous, forms flocks of up to six individuals and is a cooperative breeder (Alves 1990). Clutch size is usually two or three (Alves and Cavalcanti 1990). It is one of the few of the >800 cerrado birds whose breeding has been studied (Marini 1992; Lopes and Marini 2005a; Francisco 2006; Carvalho et al. 2007; Medeiros and Marini 2007; Marini et al. 2009a, b).

Breeding requires additional energy (over non-breeding metabolic needs) and includes risks that influence future survival (Ricklefs 1990). Clutch and egg size, and duration of incubation and nestling periods contribute to individual fitness and are subject to natural selection (Lack 1947, Ricklefs 2000a). Little is known about the natural history and breeding biology of most neotropical birds (Mason 1985, Martin 1996), especially those species endemic to restricted areas. Even less is known about the flexibility of tropical birds to changes in temporal climatic patterns (Stutchbury and Morton 2001) and global climatic conditions (Dunn 2006). Our objectives were to: (1) examine the timing of breeding and nesting cycle of the Shrike-like Tanager, and (2) learn whether these breeding parameters are flexible over time.

METHODS

Study Area.—We studied Shrike-like Tanagers in a 10,547-ha protected area (Estação Ecológica de Águas Emendadas) (ESECAE) (15° 29' to 15° 36' S, 47° 31' to 47° 41' W) in the Distrito Federal, Brazil. The protected area includes ~6,000 ha of suitable Shrike-like Tanager habitat (Duca 2007). ESECAE is one of the most important protected areas in central Brazil with 287 bird species (Bagno 1998) or 35% of the total species known for the Cerrado biome (Silva 1995). ESECAE is an isolated protected area with most nearby and surrounding areas now occupied by agriculture or housing. The local vegetation is a mosaic, ranging from grassland to dense and closed woodland, and gallery forests. The climate is markedly seasonal with the rainy season from September to April, and the remainder of the year is exceptionally dry (Nimer 1979). Details on the amount of monthly rain during this study (2003–2006) are available in Duca (2007). Biological details of ESECAE are described by Silva and Felfili (1996) and Marinho Filho et al. (1998). Urban areas and agricultural activities, and increased fire risk, are near ESECAE (SEMARH 2004).

Shrike-like Tanagers were studied mostly in 100 ha (1 x 1 km) in the interior (>1 km from
the border) of the reserve. The topography is nearly flat at an altitude ~1,040 m asl and the area is covered with a mosaic of different vegetation physiognomies typical of the Cerrado with some patches of grasslands, open cerrado, shrubby grassland, cerrado sensu stricto, and strips of gallery forest (Ribeiro and Walter 1998).

Data Collection.—We searched for nests during four breeding seasons from August to December 2003–2006. We did not search for nests during other months, but the population was monitored weekly during the entire year and no evidence of active nests was found. We captured birds weekly and recorded molt, and presence of brood patches and cloacal protuberances as indicators of reproduction. We used data on nesting activity, brood patches, and cloacal protuberances to estimate the length of the breeding period.

Active nests were checked every 3–4 days. Nests were checked every 2 days just prior to hatching and fledgling to estimate time intervals more precisely. We estimated timing of nest initiation, clutch size, and the incubation and nestling periods from these observations. The incubation period was estimated for nests found before eggs were laid and monitored until the first egg hatched. The nestling period estimation included nests with known dates of hatching and voluntary departure from the nests.

Statistical Analysis.—Means ± standard deviations are presented. Differences in clutch size among years were verified with Williams G-test. We set significance at α = 0.05 and statistical analysis followed the BioEstat 5.0 (Ayres and Ayres Jr. 2000) statistical package.

RESULTS

Breeding Period.—The Shrike-like Tanager bred from late August to early December (n = 120 nests, Fig. 1). Breeding lasted 13 weeks in 2003, 2005, and 2006, and 11 weeks in 2004. The earliest evidence of breeding was in the second week of August 2003 when a female was seen gathering nest material. The first active nests (with eggs) were found on 29 August 2003 (Fig. 1). The peak of breeding activity (most active nests) occurred in October and the last day of fledging was 10 December 2005.

The earliest nest initiation varied among years. First nests tended to be found at the start of the rainy season. The start of the breeding season varied ~30 days among the 4 years studied (Fig. 1). Breeding season length was more or less constant, regardless of timing of initiation, except in 2004. The dry season ended late in 2004, at the end of September, and breeding started later, was of shorter duration, and ended later.

Timing of observations of brood patches and cloacal protuberances during the 4 years was based on 355 captures. Females with brood patches and males with cloacal protuberances were captured from August to January, but mostly in October. Birds that were molting were captured mostly in April, but also at other times, but not in October and November (Fig. 2). Birds did not molt and have brood patches or cloacal protuberances simultaneously.

Incubation and Nestling Periods.—The incubation period ranged from 12 to 14 days in length with an average ± SD of 13.0 ± 0.7 days (n = 23). The nestling period ranged from 9.0 to 14.0 days with an average of 11.7 ± 1.4 days (n = 27) (Fig. 3). Only females were observed building nests and incubating eggs, while both males and females provisioned nestlings. Other birds in the group (helpers) were seen near nests with food in their bill, but they were not observed actually feeding nestlings.

Clutch Size.—The clutch size ranged from one to three eggs (n = 112). Clutch size in 2003 was significantly larger than in the other years: 2004, 2005, and 2006 (G = 20.028, df = 6, P = 0.003) (Fig. 4).

DISCUSSION

The breeding season of the Shrike-like Tanager is apparently flexible to changing environmental conditions and initiation of nesting can be advanced or delayed. This suggests photoperiod is not the proximal factor that stimulates onset of reproduction, but rather some type of resource, possibly food, triggers reproduction.

Breeding Period.—The breeding season of the Shrike-like Tanager is similar to that reported for other birds from southeast and central Brazil (Cavalcanti and Pimentel 1988, Piratelli et al. 2000, Marini and Durães 2001, Duca and Marini 2004, Marini et al. 2007). Other passerines nested during the same time interval at the study site, including White-rumped Tanager (Cyanpsagra hirundinacea) (Santos and Marini 2010), Black-throated Saltator (Saltator atricornis) (MAM, unpubl. data), several flycatchers (Lopes and Marini 2005a; Medeiros and Marini 2007; Marini et al. 2009a, b), and the Chalk-browed Mockingbird (Mimus saturninus) (Rodrigues 2009). The
Seasonal distribution of Shrike-like Tanager active nests and nests with eggs or nestlings at Estação Ecológica de Águas Emendadas, Brazil, from 2003 to 2006. Roman letters indicate 10-day periods of each month: I = from day 1 to 10; II = from day 11 to 20; III = from day 21 to 30 (or 31).

Peak breeding activity of the Shrike-like Tanager also coincided with that of the Red-rumped Cacique (Cacicus haemorrhous) in the Atlantic Forest (Duca and Marini 2004).

Reproduction of Shrike-like Tanagers began at the end of the dry season and beginning of the rainy season (Alves and Cavalcanti 1990). This pattern of nest initiation timing is similar to that of other passerines from southeast and central Brazil (Cavalcanti and Pimentel 1988, Marini 1992, Aguilar et al. 1999). Similarly, the beginning of the rainy season seems to be associated with reproduction in Song Wrens (Cyphorhinus phaeocephalus) in Panama (Robinson et al. 2000) and other tropical species (e.g., Aguilar et al. 2000, Mezquida 2002).

The ~30-day difference in timing of initiation of nests between 2003 and 2004 corresponds with difference in the onset of the rainy season between those years. The first rains started early in 2003

FIG. 1. Seasonal distribution of Shrike-like Tanager active nests and nests with eggs or nestlings at Estação Ecológica de Águas Emendadas, Brazil, from 2003 to 2006. Roman letters indicate 10-day periods of each month: I = from day 1 to 10; II = from day 11 to 20; III = from day 21 to 30 (or 31).
and late in 2004 with smaller differences in the other years (INMET 2006). This flexibility in nest initiation timing allows the species to cope with climatic unpredictability and, perhaps, avoid nesting in periods of low food abundance. Precipitation is known to affect the phenology of fruits (Batalha and Mantovani 2000, Batalha and Martins 2004) and insects (Diniz and Morais 1997, Pinheiro et al. 2002) in the Cerrado.

The breeding period (~13 weeks) is short, compared to that of tropical forest birds (reviewed by Stutchbury and Morton 2001). The finding of some birds with brood patches in January suggests the breeding season may end later than December in some years. This short breeding season is similar to that for birds breeding in the Cerrado (Marini and Durães 2001; Lopes and Marini 2005a; Medeiros and Marini 2007; Marini et al. 2009a, b; Rodrigues 2009; Santos and Marini 2010). Despite the short breeding season, Shrike-like Tanagers usually attempted to nest more than once in the same breeding season, and had high adult survival and low fecundity (Duca 2007). Tropical birds have long breeding seasons compared to temperate species (reviewed by Stutchbury and Morton 2001). This does not apply in several highly seasonal tropical environments, such as the cerrado, pantanal wetlands (Pinho 2005), and caatinga dry forests (CD, pers. obs.). Harsh climatic (e.g., prolonged dry periods in the cerrado or caatinga) or environmental (e.g., flooding in the pantanal) conditions may last at least 4 months and constrain the time available for breeding and molt in a similar context as in temperate regions.

**Incubation and Nestling Periods.** The incubation period of the Shrike-like Tanager was ~15-30% shorter than that (15-17 days) reported in another area 40 km from our study site (Alves and Cavalcanti 1990). This difference in the incubation period might be explained by methodological or year differences or small sample sizes. The incubation period we documented is similar to that reported for the Lesser Elaenia (Elaenia chiriquensis) (13.4 days) (Medeiros and Marini 2007) and Black-throated Saltator (14 days).
The Shrike-like Tanager nestling period (11.7 days) was ~20% longer than that (9.5 days; n = 4) estimated by Alves and Cavalcanti (1990). Random variation in nestling period among the few nests they studied may account for this difference. This short nestling period is similar to that reported for the White-rumped Tanager (12.1 days) (Santos and Marini 2010) and Wedge-tailed Grass Finch (11.3 days; MAM, unpubl. data) at the same study site. It is much shorter than reported for the Black-throated Saltator (14 days) (MAM, unpubl. data) or several flycatchers (15 to 18.9 days) in the same study area (Lopes and Marini 2005a; Medeiros and Marini 2007; Marini et al. 2009a, b). The short nestling period for the Shrike-like Tanager and other species may be related to high nestling mortality rates that could be a selective factor favoring high growth rates and a short nestling period (Ricklefs 1976, Alves and Cavalcanti 1990). Some species leave the nest earlier than others (Willis 1961), which may be related to ground feeding habits (Alves and Cavalcanti 1990).

Only females built nests and incubated eggs. Both males and females, and probably helpers, provisioned nestlings as reported by Manica (2008). These behaviors are similar to those of another population of Shrike-like Tanager (Alves 1990, Alves and Cavalcanti 1990) and the White-rumped Tanager in the same study area (Santos and Marini 2010).

**Clutch Size**.—The clutch size (~2) for the Shrike-like Tanager is similar to that for tanagers in South America (Alves and Cavalcanti 1990, Yom-Tov et al. 1994). Explanations for small clutch size of tropical species are possibly related to cost of egg production and raising young, as well as climatic variation in temperature, air humidity, and photoperiod (reviewed by Ricklefs 1991). However, these small differences in the incubation period may change temporally and in response to changes in environmental conditions and food availability (Murphy 1986, Rotenbery and Wiens 1991).

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**LITERATURE CITED**


PINHO, J. B. 2005. Diversidade de espécies, padrões de migração e biologia reprodutiva de Aves em quatro ambientes florestais do Pantanal de Poconé, MT. Thesis. Universidade Federal de Minas Gerais, Cuiabá, Brazil.


ARCTIC FOXES, LEMMINGS, AND CANADA GOOSE NEST SURVIVAL AT CAPE CHURCHILL, MANITOBA

MATTHEW E. REITER1,3,4 AND DAVID E. ANDERSEN2

ABSTRACT.—We examined factors influencing Canada Goose (Branta canadensis interior) annual nest success, including the relative abundance of collared lemmings (Dicrostonyx richardsoni), arctic fox (Alopex lagopus) den occupancy, nest density, and spring phenology using data collected during annual Canada Goose breeding area surveys at Cape Churchill, Manitoba. Nest density and arctic fox den occupancy strongly influenced Canada Goose nest success. High nest density resulted in higher nest success and high den occupancy reduced nest success. Nest success was not influenced by lemming abundance in the current or previous year as predicted by the "bird-lemming" hypothesis. Reducing arctic fox abundance through targeted management increased nest survival of Canada Geese; a result that further emphasizes the importance of arctic fox as nest predators in this system. The spatial distribution of nest predators, at least for dispersal-nesting geese, may be most important for nest survival, regardless of the abundance of small mammals in the local ecosystem. Further understanding of the factors influencing the magnitude and variance in arctic fox abundance in this region, and the spatial scale at which these factors are realized, is necessary to fully explain predator-prey-alternative prey dynamics in this system. Received 22 June 2010. Accepted 5 January 2011.

Substantial inter-annual variation occurs in reproductive parameters of many arctic and subarctic nesting geese (Bruggink et al. 1994, Gleason et al. 2004). Factors influencing this variation include annual weather fluctuations (Ryder 1970, Raveling and Lumsden 1977, Reiter 2009) and changes in predator pressure (Angelstam et al. 1984, Summers 1986, Béty et al. 2001). Late onset of snow melt and spring phenology directly affects condition of female geese resulting in low nest densities and increased nest failure (Ryder 1970, Moser and Rusch 1998). Variation in nest success from changes in predator pressure is likely more complex and often involves the dynamic interaction of potential nest predators with their primary and alternative prey (Angelstam et al. 1984, Summers 1986). Understanding these inter-specific associations in a predator-prey system requires consideration of the spatial scale at which inter-specific interactions occur.

The alternative-prey hypothesis refers to predator-prey relationships where predators specialize on primary prey until that prey population declines below a threshold density, at which point they functionally respond and consume alternative prey (Angelstam et al. 1984). This behavior typically occurs when the predator is specialized and experiences reduced fitness with declining primary prey. However, the form of the functional response of the predator to changes in abundance of primary and secondary prey may vary depending on the spatial distribution and abundance of the alternative prey resource, as well as the relative cost of migrating in search of alternative food concentrations (Angerbjörn et al. 1999).

Annual variation in nest success of arctic-nesting birds and the relationship with small mammals ("bird-lemming" hypothesis) has been recognized in northern Russia and Europe (Angelstam et al. 1984, Summers 1986) and in North America (Wilson and Bromley 2001; Béty et al. 2001, 2002). Arctic fox (Alopex lagopus) and other predators specialize in feeding on primary prey, lemmings (Dicrostonyx spp., Lemmus spp.), under the apparent-competition theory of this hypothesis and increase reproduction when lemmings are abundant. Predators switch to feeding on alternative prey including ground-nesting birds and bird eggs in years when lemming abundance is low. Subsequently, ground-nesting birds are predicted to experience reduced reproductive performance in the year following a lemming peak when arctic fox are abundant, but likely recover in subsequent years as predator populations decline (Angelstam et al. 1984, Summers 1986). This theoretical hypothesis has been corroborated with some empirical data from large colonies of arctic-nesting birds (e.g., Béty et al. 2002), but few studies have assessed the bird-lemming hypothesis in relation to dispersed-
Eastern Prairie Population (EPP) Canada Geese (Branta canadensis interior) at Cape Churchill, Manitoba have exhibited substantial inter-annual variation in nest success over nearly 30 years (1976-2004). Arctic fox depredation accounts for >80% of nest failures in some years (Walter 1996) and local arctic fox dens have been monitored regularly for occupancy. Multi-annual cycles have been documented in collared lemming (Dicrostonyx richardsoni) populations, a primary prey of arctic foxes in this area (Bahr 1989), near the town of Churchill (Shelford 1943, Scott 1993) and more recently at Cape Churchill (Roth 2003, Reiter and Andersen 2008b). However, the extent to which annual fluctuations in nest success of dispersed-nesting EPP Canada Geese coincide with variation in lemming abundance and arctic fox den occupancy is unknown. We used existing data from Cape Churchill, Manitoba between 1993 and 2004 to quantify factors influencing Canada Goose nest success in the context of the predictions of the bird-lemming hypothesis. We (1) present time-series of Canada Goose nest success, nest density, hatch date, relative arctic fox abundance, and relative abundance of lemmings between 1993 and 2004; and (2) model nest success as a function of years with peak lemming abundance, years with a lemming population trough 1 year following a peak, arctic fox den occupancy, nest density, and median hatch date. We also examined the impact of fox removal, which occurred on our study area from 1994 to 1997, on nest success.

METHODS

Study Area.—The EPP Canada Goose breeding range includes ~101,500 km² in northern Manitoba, Canada (Malecki et al. 1980). The highest density of breeding Canada Geese occurs along a strip of coastal tundra on western Hudson Bay within the broader ecosystem of the Hudson Bay Lowlands (Reiter 2009). The Nestor One study area (~48 km²; 58°34' N, 93°11' W) was south of Cape Churchill and ~60 km east-southeast of the town of Churchill, Manitoba (Fig. 1). Nestor One is characterized by low relief, continuous permafrost, and coastal tundra vegetation (Didiuk and Rusch 1979, Brook 2001). Coastal salt marshes, beach ridges, sedge (Carex spp., Eriophorum spp.) meadows, and interior sedge meadow complexes comprise the major habitat types. The northern boreal forest ecosystem is ~10 km inland from Nestor One and the Hudson Bay coastline.

Arctic fox breed in relatively high densities on the coastal tundra in this region, using established dens along large, elevated beach ridges (Bahr 1989, Roth 2003). Collared lemmings, the only lemming or vole species that occur on the Nestor One study area (Roth 2002), are the primary food for arctic foxes. Nesting waterfowl (Anseriformes) and shorebirds (Charadriiformes) are abundant in this region and are consumed by foxes (Bahr 1989; M. E. Reiter, unpubl. data) during the summer. A breeding colony of >20,000 nesting Lesser Snow Geese (Chen caerulescens caerulescens) and Ross's Geese (C. rossii) occurs <20 km from Nestor One at La Pérouse Bay (Fig. 1; Cooke et al. 1995).

Nest Success and Hatch Date.—Ground surveys of Canada Goose nests and estimates of nest survival were completed annually at Nestor One since 1976 following standardized protocols (Didiuk and Rusch 1979, Walter 1999). Nest-search crews (4-6 people) spaced at regular intervals systematically searched Nestor One. Females were flushed at all nests encountered and the incubation day of the nest was estimated using candling and flotation methods (Westerkov 1950, Weller 1956, Reiter and Andersen 2008a). Nest locations were marked with a 7.5 × 12.5-cm plastic orange flag placed 10 m north of the nest bowl. We revisited nests at or subsequent to predicted hatch date, based on a 28-day incubation period, to ascertain fate (Didiuk and Rusch 1979, Walter 1999). We categorized nests as (1) successful if ≥1 egg hatched, indicated by the presence of goslings in the nest or eggshells and intact membranes consistent with hatching, or (2) failed if few or no eggshell fragments were in the nest. We calculated daily survival rate (DSR) and annual nest success using exposure days and the number of nests that failed after initial discovery (Mayfield 1975). We followed methods described by Johnson (1979) to construct 95% confidence intervals (95% CI) for DSR and nest success. We also estimated the median hatch date for all Canada Goose nests in each year as a measure of spring phenology, as hatch date is correlated with timing of snow melt (Walter 1999).

Nest Density.—We calculated nest density for each year from 1993 to 2004 as the number of Canada Goose nests/100 ha of wetland nest habitat. We used estimates from Walter and Rusch (1997) to correct observed nest counts for...
probability of detection. We divided the number of active nests and failed nests at discovery by 0.77 and 0.39, respectively; the average probability of detection estimates based on a 2-year study of EPP nest-searching methods. We calculated the 95% CI of estimates of the detection probabilities using the mean ± 2 SD (0.029 and 0.053 for active and failed nests, respectively) as reported in Walter and Rusch (1997); and generated a 95% CI for nest density in each year.

Lemming Abundance.—We used relative lemming abundance estimated by Reiter and Andersen (2008b) for Nestor One between 1992 and 2004 to identify years with lemming population peaks and
TABLE 1. Variables considered in models of nest success of Eastern Prairie Population Canada Geese in northern Manitoba, Canada and predicted associations under the “bird-lemming” hypothesis. The predicted association for hatch date (HATCH) and nest density (D) with nest success was based on previous studies of factors influencing nesting Canada Geese (positive = good goose condition; negative = more predators).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Predicted association with nest success</th>
</tr>
</thead>
<tbody>
<tr>
<td>LP</td>
<td>Peak lemming year (1 = peak; 0 = other)</td>
<td>Positive</td>
</tr>
<tr>
<td>LT</td>
<td>Trough lemming year, 1-year following peak (1 = trough, 0 = other)</td>
<td>Negative</td>
</tr>
<tr>
<td>FD</td>
<td>Fox den occupancy</td>
<td>Positive</td>
</tr>
<tr>
<td>D</td>
<td>Density of nests/100 ha of wetland</td>
<td>Positive or Negative</td>
</tr>
<tr>
<td>HATCH</td>
<td>Median hatch date (1 Jun = 1)</td>
<td>Negative</td>
</tr>
<tr>
<td>T</td>
<td>Trapping of arctic fox (1 = trap, 0 = no trap)</td>
<td>Positive</td>
</tr>
</tbody>
</table>

Reiter and Andersen (2008b) adapted methods described by Danell et al. (1999) to generate a relative measure of lemming abundance. This index was calculated by collecting a random sample of scars on willow (Salix spp.) plants caused by lemming feeding, quantifying the distribution of scar ages using dendrochronological techniques, and modeling the distribution of scar ages using non-linear Poisson regression. The model-based correction was necessary because distribution of scar ages collected in a single year was biased as older scars were harder to detect because of plant growth and there were relatively fewer older scars due to natural plant death. The units of this index were the predicted number of scars of each scar age that would be counted if all scars were equally detected and no plants died. This method estimated relative lemming abundance from the end of the previous plant growing season to the following spring in each year on the Nestor One study area for a period of years extending through the age of the oldest scar. Previous studies found that small mammal population indices for winter to spring using scar analysis were proportional to small mammal captures in the subsequent summer months (Erlinge et al. 1999, Predavec et al. 2001). We defined a year of peak lemming abundance (LP) as a year when the relative abundance of lemmings was one standard deviation (SD) larger than the long-term mean (1992–2004). We classified the year following a peak as a lemming trough (LT) when there was a 2 SD decline from the abundance in the previous peak year. LP and LT were included separately in models as factors (Table 1).

Fox Den Occupancy.—We visited arctic fox dens (FD) on and near the study area as part of annual EPP Canada Goose research activities. We evaluated dens for evidence of recent (i.e., since snow melt) activity based on the presence of foxes or fresh fox sign (e.g., digging, prey remains, or scat; Macpherson 1969) indicative of an occupied den. We calculated the proportion of occupied dens each year for 1993 to 2004, and the 95% CI for the proportion of occupied dens in each year using the percentile method and the distribution of 1,000 bootstrapped estimates of fox den activity (Efron and Tibshirani 1993).

Dens were surveyed only once during nest-searching activities in 1993–2004; thus, it was unclear whether fresh activity actually indicated an occupied den (i.e., the den was occupied by foxes for the entire goose nesting season and not just visited by foxes prior to our visit). Our definition of this covariate was important for interpreting our data as related to the bird-lemming hypothesis. This hypothesis predicts the proportion of dens with fresh activity should be negatively associated with annual nest success if den activity was an index to relative fox abundance. However, if den activity was considered a measure of den occupancy, which should be high when lemmings were abundant and if lemmings buffer bird nests against predation, our fox den covariate would be predicted to be positively associated with nest success (Table 1). We used data collected during repeated visits to arctic fox dens in 2004–2007 to test the ability of fresh fox sign during the first visit to successfully predict occupancy. These results suggested the proportion of dens with fresh activity at first visit was positively correlated (Pearson’s correlation coefficient, \( r = 0.82, n = 4 \) years) with den occupancy, and we considered our fox den data to represent den occupancy.

Statistical Analyses and Hypotheses.—We calculated summary statistics for all variables in our analysis and used autocorrelation functions (Box and Jenkins 1976) as preliminary assessments of
cycling for all variables. All autocorrelation functions were evaluated at the $z = 0.05$ significance level. We developed 17 regression models a priori, based upon previously published descriptions of predator-prey-nest success dynamics under the bird-lemming hypothesis (Summers 1986, Béty et al. 2002). We fit models using maximum-likelihood, ranked competing models using Akaike’s Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002), and compared among models using Akaike weights ($w_i$); interpreted as the probability the $i^{th}$ model was the best, given the data, and the set of models evaluated. We calculated the difference between the top model (lowest AICc) and all other models ($\Delta_i$) and considered models $\leq 2 \Delta_i$ to be in the top model set. We estimated a pseudo-$R^2$ as $1 - \frac{\text{deviance of the } i^{th} \text{ model/ the deviance of the intercept-only model}}{\text{deviance of the intercept-only model}}$ to quantify the amount of variation in the data accounted for by our best model (Cameron and Windmeijer 1996).

Peak lemming years (LP) are predicted to be positively correlated with nest success (Table 1) and fox den occupancy under the bird-lemming hypothesis. However, trough lemming (LT) years, 1 year following a peak lemming year, are predicted to be negatively correlated with nest success in the current year (Table 1). We predicted nest density (D) would be negatively correlated with nest success (Table 1) if high nest density increased fox den occupancy (FD) and predation pressure. However, nest density and nest success are also likely influenced by annual fluctuations in spring phenology. We predicted that median hatch date (HATCH; standardized to 1 Jun = 1) should be negatively correlated with nest success (Table 1).

We considered three models that included a categorical variable (T) indicating whether fox removal occurred (1994–1997) to evaluate the effect fox removal had on nest success and also indirectly the influence of arctic fox abundance. Fox removal was used as part of an experiment to manipulate fox predation pressure on nesting Canada Geese and consisted of a concerted effort to trap or shoot all fox on the study area beginning in late April and continuing through the median hatch date for Canada Geese (Walter 1996, 1999). We predicted arctic fox removal would reduce the number of nest predators on the study area resulting in higher nest success.

We used analysis of variance (ANOVA) and Spearman rank correlation tests, post hoc, to evaluate assumed associations among covariates under the bird-lemming hypothesis (Hollander and Wolfe 1999). Data summaries are presented as mean $\pm$ SD. We used Program R, Version 2.11 (R Development Core Team 2010) for all statistical analyses.

Our measure of arctic fox den occupancy was based on $\geq 10$ surveyed dens in all but 1 year; however, 95% CIs for the proportion of occupied fox dens were large. We conducted a simulation to quantify the influence of uncertainty in our fox den occupancy covariate estimates in each year on our model selection results and fox den coefficient values. We selected 200 random samples with replacement from the fox den data for each year, 1993–2004. The sample size in each simulated year was equal to the sample size observed for that year, and resulted in a vector of 1s (occupied den) and 0s (unoccupied den). The proportion of occupied fox dens was calculated for each year for that iteration of the fox den data. These simulated fox den covariate data for each year were included in an analysis of all 17 a priori models and the models were ranked based on $\Delta_i$. This simulation produced 800 $\Delta_i$ and 800 fox den coefficient ($\beta$) estimates; 200 of each for every model ($n = 17$) where it occurred. We calculated the proportion of 200 iterations where the FD covariate was included in the top model ($\Delta_i = 0$) or top model set ($\Delta_i \leq 2$) as a measure of model selection uncertainty caused by high variance in FD covariate estimates. We also considered the 20th and 780th ranked values of all simulated coefficient estimates for FD to represent the 95% CI of this parameter. We concluded the coefficient estimates were not sensitive to uncertainty in the covariate data used in the analysis if the 95% CI did not overlap 0.

**RESULTS**

**Nest Success and Covariates.**—Estimated probability of Canada Goose nest success, derived from, on average, 165 $\pm$ 64 nests per year (min = 24, max = 230), ranged from 0.01 to 0.85 with a mean of 0.48 $\pm$ 0.27 between 1993 and 2004. Estimates of nest success exhibited substantial annual variation (Fig. 2A) although autocorrelation functions indicated no statistically significant correlations in nest success among years (Fig. 3A). Nest density at Nestor One ranged from 1.23 to 12.22 nests/100 ha of wetland nesting habitat with a mean of 7.92 $\pm$ 2.95 between 1993 and 2004. Nest density had low variation and was declining
in the mid-1990s but has become more variable in recent years (Fig. 2B). The autocorrelation function provided no evidence of regular cycles between 1993 and 2004 (Fig. 3B). Median hatch date ranged from 13 June to 11 July and averaged 26 June. Median hatch date has become more variable in recent years (Fig. 2C) but exhibited no significant evidence of regular cycles (Fig. 3C). Nest density and median hatch date were negatively correlated ($\rho = -0.49, P = 0.10$), as years with late hatch dates tended to have lower nest density.

We identified five peak lemming population years (1995, 1998, 2000, 2001, 2003) and four lemming trough years, 1 year following a peak (1993, 1996, 1999, 2002) between 1993 and 2004. This was based on our index to relative lemming abundance (i.e., predicted number of willow scar age counts per year) which ranged from 72 to 477 with a mean of $279 \pm 150$. Relative lemming abundance cycled with a periodicity of 3 years at Nestor One during 1993–2004 (Fig. 2D), and the autocorrelation function identified significant positive correlation in lemming abundance at 3-year intervals between 1993 and 2004 (Fig. 3D).

The proportion of occupied fox dens ranged from 0.13 to 0.91 between 1993 and 2004 and averaged $0.61 \pm 0.25$. The total number of dens
FIG. 3. Autocorrelation function plots (1993-2004) for: (A) Canada Goose nest success, (B) Canada Goose nest density, (C) median hatch date, (D) relative abundance of collared lemmings, and (E) proportion of occupied arctic fox dens near Cape Churchill, Manitoba. Lag values are in years (0 = current year, thus autocorrelation = 1). Dashed lines represent $\alpha = 0.05$ significance level.

surveyed in each year ranged from four to 17 resulting in substantial variation in width of the estimated 95% CI for the proportion of occupied dens (Fig. 2E). The autocorrelation function indicated no cycling between 1993 and 2004 (Fig. 3E). There was no significant association between the proportion of occupied fox dens and LP ($F_{1,10} = 0.28, P = 0.61$ or LT ($F_{1,10} = 1.18, P = 0.30$) and no significant association between occupied arctic fox dens and nest density ($\rho = 0.29, P = 0.35$). Our data suggested that arctic fox den occupancy was influenced by fox removal efforts. There was a lower ($F_{1,10} = 12.5, P < 0.005$) proportion of fox dens occupied in years with (1994-1997) than in years without fox removal (1998-2004).

**Model Summary.**—We considered 17 models in our analysis (Table 2) and all models contained an intercept term ($\beta_0$). The model including nest density and fox den occupancy received substantial support as the best among those evaluated (Table 2). None of the other models was $\leq 2$ AICc units from the top model. The top model received 0.61 of the Akaike weight ($w_0$), over three times more support than the next-best-supported model. The top model had a pseudo-$R^2$ of 0.64. The top six models, which included the top model, a model with the fox trapping effect and nest density, a model with median hatch date and the fox trapping effect, and the single-factor models of nest density, fox den occupancy, and the fox trapping effect had a cumulative AICc weight of 0.91 (Table 2). Coefficient estimates from the top model indicated a positive relationship between nest density and nest success ($\beta_D = 0.05; 95\% \text{ CI: } 0.01, 0.10$); an increase of one goose nest/100 ha on average, increased nest success by 0.05. The proportion of occupied fox dens was negatively associated with nest success ($\beta_P = -0.64; 95\% \text{ CI: } -1.14, -0.15$). An increase of 0.10 in the proportion of occupied dens (~1 additional occupied den) decreased nest success by 0.06. Fox trapping, based on the second best-supported model, had a positive effect on nest success. Nest success in years when fox were trapped increased by 0.28 (95% CI: 0.04, 0.56). FD was included in the best-supported model ($\Delta_i = 0$) or top model set ($\Delta_i \leq 2$) in 87% ($n = 173$) of iterations in our post-hoc simulation. This model was usually the same as the top model from the original analysis.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta_i$</th>
<th>$w_0$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D + FD$</td>
<td>-2.27</td>
<td>0.00</td>
<td>0.61</td>
</tr>
<tr>
<td>$D + T$</td>
<td>0.28</td>
<td>2.55</td>
<td>0.17</td>
</tr>
<tr>
<td>$HATCH + T$</td>
<td>2.95</td>
<td>5.22</td>
<td>0.04</td>
</tr>
<tr>
<td>FD</td>
<td>3.79</td>
<td>6.06</td>
<td>0.03</td>
</tr>
<tr>
<td>$D$</td>
<td>3.79</td>
<td>6.06</td>
<td>0.03</td>
</tr>
<tr>
<td>$T$</td>
<td>3.98</td>
<td>6.25</td>
<td>0.03</td>
</tr>
<tr>
<td>$HATCH + FD$</td>
<td>4.05</td>
<td>6.33</td>
<td>0.03</td>
</tr>
<tr>
<td>$D + LT$</td>
<td>4.56</td>
<td>6.83</td>
<td>0.02</td>
</tr>
<tr>
<td>$D + LP$</td>
<td>5.34</td>
<td>7.61</td>
<td>0.01</td>
</tr>
<tr>
<td>$FD + LT$</td>
<td>5.55</td>
<td>7.83</td>
<td>0.01</td>
</tr>
<tr>
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<td>8.20</td>
<td>0.01</td>
</tr>
<tr>
<td>LT</td>
<td>6.11</td>
<td>9.18</td>
<td>0.01</td>
</tr>
<tr>
<td>$HATCH$</td>
<td>7.26</td>
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<td>$HATCH + LT$</td>
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<tr>
<td>$HATCH + LP$</td>
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<td>11.52</td>
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</tr>
</tbody>
</table>

Table 2. Regression analysis for nest success of Eastern Prairie Population Canada Geese in northern Manitoba, Canada. Models were ranked using Akaike's Information Criterion corrected for small sample size ($AICc$) and compared using differences in $AICc$ ($\Delta_i$) and Akaike weights ($w_0$). $k =$ number of model parameters. All models included an intercept term. Variable definitions are in Table 1.
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Figure 4. Frequency of 800 coefficient estimates for the association of the proportion of occupied arctic fox dens (FD) with EPP Canada Goose nest success from 200 random iterations of arctic fox den data and evaluation of four models with FD included.

The second-best-supported model from the original analysis was the only other to be selected as the top model (39% of iterations) and included the fox trap effect, another index to fox abundance. Coefficient estimates for fox dens (p > 0; n = 800) from our simulation were not >0 and the 95% CI was -0.61 to -0.39 (Fig. 4). These diagnostic simulations suggest that uncertainty in our estimates of the proportion of occupied fox dens in each year did not significantly influence model selection or inference regarding the influence of fox den occupancy on Canada Goose nest success.

DISCUSSION

Nest success of dispersed-nesting Canada Geese in our study area within a subarctic coastal-tundra trophic ecosystem near Cape Churchill, Manitoba, exhibited substantial year-to-year variation in the mid 1990s and early 2000s. Arctic fox den occupancy and nest density were both significantly associated with Canada Goose nest success. Our best supported model of Canada Goose nest success, however, was not consistent with predictions of the bird-lemming hypothesis, as higher arctic fox den occupancy lowered nest success and was not related to lemming abundance. Walter (1999) reported that increased nest predation by arctic fox was the primary cause of low nest success at Nestor One in the 1980s. Our assessment of the effects of arctic fox supports the contention that foxes are a primary predator of nests in this system and, after spring phenology (presumably as it influences nest density, hatch date, and the condition of nesting geese), arctic fox are an important factor influencing Canada Goose nest success. The mechanisms driving changes in the fox population in this ecosystem, which we were unable to directly link with lemming abundance and the bird-lemming hypothesis, have important consequences for nesting Canada Geese and likely other birds that nest along western Hudson Bay.

Arctic fox den occupancy varied among years, although non-cyclically. This is consistent with reports of variation in arctic fox reproductive behavior elsewhere where primary food resources fluctuate (Macpherson 1969, Elmhagen et al. 2000, Strand et al. 2000). Lemming abundance fluctuated cyclically (as postulated under the bird-lemming hypothesis) on our study area, but was not included in our best-supported model of Canada Goose nest success. We were unable to identify an association between arctic fox den occupancy and peak lemming years as predicted by the bird-lemming hypothesis. Our results were consistent with those of Bromley et al. (1998) who found reduced nest survival of Cackling Geese (Branta hutchinsii) during high fox years in the Northwest Territories, Canada, and with Reiter (2009) who identified high den occupancy in high lemming years and lower Canada Goose nest survival at Cape Churchill (2005–2008). Our data also suggest arctic fox removal was effective at increasing Canada Goose nest success, supporting previous research that identified arctic fox as a critical component influencing nest success in this system (Walter 1996, 1999).

Our results, similar to Béty et al. (2001) and Miller et al. (2007), indicate density of nesting geese was positively associated with nest success. This positive association was either the result of (1) early spring phenology and nesting geese in good physiological condition, which allowed for more time to tend nests and more effective defense of nests against predation; (2) a higher density of goose nests that induced group defense against arctic fox; or (3) a combination of these two factors. The evolution of dispersed nesting ecology by Canada Geese may be the result of the individual defensive capabilities of adult Canada Geese; a nesting pair often can successfully defend their nest against arctic fox (Bahr 1989). Group defense has rarely been observed in nesting
Canada Geese, as strong territoriality is more common (Mowbray et al. 2002, Reiter 2009). The lack of association between nest density and fox den occupancy combined with evidence of a strong correlation of nest density and hatch date in our study suggested that spring phenology and nesting geese in good physiological condition (as represented by nest density and hatch date) best described among-year variation in success of dispersed Canada Goose nests.

The bird-lemming hypothesis and, more generally, the alternative-prey hypothesis as applied to the system we studied, assumes arctic fox populations specialize on lemmings when lemmings are abundant, functionally respond and switch to nesting birds when lemmings decline, and this interaction occurs at some relevant spatial scale. Arctic fox, under this assumption, are present and depredate goose nests even when lemming abundance has declined. However, if alternative prey, particularly nesting birds, is not abundant when lemming abundance decreases, foxes may not breed and become nomadic or substantially increase the size of their home range (Wrigley and Hatch 1976, Eberhardt et al. 1983, Eide et al. 2004). The extent of increased arctic fox mortality or emigration and the magnitude of a decline in fox abundance, following a lemming peak, likely depends on timing of the lemming population crash (Tannerfeldt et al. 1994, Angerbjörn et al. 1999), abundance of alternative food resources (natural [Roth 2003] or man-made [Eberhardt et al. 1982, 1983]), prevalence of disease (Kaplan 1985, Ballard et al. 2001), and how foxes respond to these factors.

The relationship between arctic fox abundance and changes in lemming abundance may be confounded by the effects of alternative prey resources off our study area. Bahr (1989) reported high year-to-year variability in the presence of lemmings in the arctic fox diet at Nestor One, but little variability in the presence of adult geese or goose eggs. This suggests arctic fox are lemming specialists and do not compensate for reduced lemming abundance through increased consumption of goose eggs on the Nestor One study area. The La Pérouse Bay Lesser Snow Goose and Ross's Goose colony, which is <20 km from Nestor One and has >20,000 nesting pairs of Snow and Ross's geese, provides a much higher density of potential food for arctic fox than Canada Geese at Nestor One, when lemming abundance is low. Human habitation sites may also attract foxes during low primary prey years (Eberhardt et al. 1982, 1983). The town of Churchill, Manitoba is <60 km from our Cape Churchill study area and may provide a reliable, concentrated food resource (e.g., an open dump; which operated during our study) for arctic foxes. The magnitude of the effect of variation in predator abundance and their primary prey (lemmings) on alternative prey (goose eggs) may change depending on whether the functional response of predators is to remain in the local area, switching to bird nests (i.e., a closed predator population), or to disperse following a decline of lemmings. Ultimately, predator, prey, and alternative-prey dynamics in this system may be operating at a larger spatial scale than our study area, highlighting the importance of considering spatial scale when evaluating the bird-lemming hypothesis.

Nest success of Canada Geese near Cape Churchill exhibited strong annual variation and high arctic fox den occupancy was associated with low nest success. Previous studies of predator pressure on northern nesting geese in simple trophic systems supported the predictions of the bird-lemming hypothesis (Wilson and Bromley 2001; Béty et al. 2001, 2002) with geese experiencing reduced nest survival in years following a lemming peak. Our relatively long-term study (12 years) was conducted in a landscape inhabited by geese with dispersed-nesting ecology and our results were not consistent with predictions of the bird-lemming hypothesis. We suggest that, at least for dispersed-nesting geese, the spatial distribution of predators may be most important to nest survival, regardless of the abundance of small mammals in the local ecosystem. Further research is needed to understand factors influencing the spatial distribution and abundance of arctic fox, particularly in light of rapidly increasing numbers of Lesser Snow Geese and Ross's Geese throughout this region of arctic and subarctic Canada (Jeffries et al. 2006), and the appropriate spatial scale at which to evaluate the dynamics of these trophic interactions.

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and Bob Reside. We thank B. E. Reichert, Tim Pearson, D. H. Rusch, B. W. Allen, S. E. Walter, and R. R. Nock in addition to the many volunteers who assisted in field data collections over many years at Nestor One. We thank T. W. Arnold, F. B. Martin, J. S. Lawrence, and two anonymous reviewers for comments that greatly improved this manuscript. This research was conducted in accordance with all applicable state, provincial, and federal regulations. Use of trade names does not imply endorsement by either the U.S. Geological Survey or the University of Minnesota.

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GIANT COWBIRD (*MOLOTHRUS ORYZIVORUS*) PARASITISM OF RED-RUMPED CACIQUES (*CACICUS HAEMORRHOUS*) IN THE ATLANTIC FOREST, NORTHEASTERN ARGENTINA

ROSENDO M. FRAGA

ABSTRACT.—Host-parasite interactions between Red-rumped Caciques (*Cacicus haemorrhous*) and Giant Cowbirds (*Molothrus oryzivorus*) were studied at 52 nests in the Atlantic Forest, Misiones, Argentina. Cowbird eggs (1–6) occurred in 27 of 38 cacique nests (71%) found during the egg stage. Giant Cowbird eggs were white and unmarked (85%), or marked and spotted over pale buff (15%); the marked eggs somewhat resembled host eggs, but were twice as large. Four host and three parasite eggs were found punctured and broken. Only three cowbird nestlings were observed, and resembled oropendola (*Psarocolius* spp.) nestlings more than those of Red-rumped Caciques. Botflies (*Philornis* spp.) infested cowbird and cacique nestlings, but there was no evidence of a cowbird-cacique preening mutualism.

The Giant Cowbird (*Molothrus oryzivorus*) is an obligate brood parasite in the New World tropics from Mexico to Argentina. Its better-known hosts are colonial nesting species of caciques (*Cacicus*) and oropendolas (*Psorocolius*) (Friedmann 1963, Robinson 1988, Jaramillo and Burke 1999). Host-parasite interactions of Giant Cowbirds have been mostly studied in Costa Rica (Crandall 1914, Webster 1994, Cunningham and Lewis 2006), Panama (Smith 1968, 1980), Venezuela (Haverschmidt 1966, 1967), and Peru (Robinson 1988). However, field research on breeding of this cowbird has not been extensive. Commonly the nests of its cacique and oropendola hosts are inaccessible (Webster 1994), as colonies are built in the upper branches of tall isolated or emergent trees (Fraga 1989, Jaramillo and Burke 1999) and, at times, near nests of aggressive wasps or bees (Smith 1968). Important information on interactions of Giant Cowbirds and their hosts was obtained by Smith (1968, 1980) and Fleischer and Smith (1992) in Panama.

Smith (1968) reported an unusual and complex interaction between Giant Cowbirds and two hosts in Panama, the Chestnut-headed Oropendola (*Psarocolius wagleri*) and the Yellow-rumped Cacique (*Cacicus cela*). The interaction included possible cases of mutualism and egg mimicry (Smith 1968, 1980). Preening mutualism was reported when nestlings of Chestnut-headed Oropendolas were infested by ectoparasitic botfly larvae (*Philornis* spp.) that could cause nestling mortality. Giant Cowbird nestlings apparently removed the larvae from themselves and their nest mates in botfly-infested broods, and were beneficial to the host. Botfly infestations were not found in host colonies built near nests of aggressive wasps. The cowbird nestlings competed with host nestlings in these instances, and host adults were aggressive to the brood parasites. Hosts removed cowbird eggs not resembling their own in wasp-protected colonies, but incubated those with mimetic resemblance.

Subsequent studies by Robinson (1988) did not find evidence of preening mutualism in Peruvian hosts including Yellow-rumped Caciques and Russet-backed Oropendolas (*Psarocolius angustifrons*), which were invariably aggressive to Giant Cowbirds. Webster (1994) also reported constant host aggressiveness to Giant Cowbirds in colonies of Montezuma Oropendolas (*P. montezuma*) in Costa Rica.

Giant Cowbirds in Argentina, according to Jaramillo and Burke (1999), are found only in northern Misiones Province, where the only potential host is the colonial nesting Red-rumped Cacique (*Cacicus haemorrhous*). A Giant Cowbird egg was once reported from a nest of Red-rumped Caciques in Amazonian Brazil (Pinto 1953), but recent studies on the cacique in eastern Brazil (Duca and Marini 2004, 2008, Pizo 2009) did not report parasitism. De la Peña (1987) also reported one Giant Cowbird egg in one nest of Red-rumped Caciques from Misiones, Argentina, but cowbird interactions with this host remain unstudied.

My objectives are to: (1) provide the first account of the host-parasite interaction between Red-Rumped Caciques and Giant Cowbirds. (2)
compare this interaction with previous studies of Giant Cowbirds and other hosts with particular emphasis on the possible egg and nestling mimicry by the parasite, and (3) evaluate the possible occurrence of a preening mutualism between caciques and cowbirds.

METHODS

I had field experience with Giant Cowbirds, their eggs and nestlings, in Panama and Costa Rica in 1985–1986 (Fraga 1989). I also had access to the extensive collection of eggs of this cowbird at the Smithsonian Tropical Research Institute obtained by N. G. Smith. Information on the Argentinean distribution of Giant Cowbirds and data on colony sizes of Red-rumped Caciques were obtained during field trips to Corrientes and Misiones provinces (1995–2007), and from the literature and museum specimens. Red-rumped Cacique nests (n = 52) from eight colonies were studied between October 1995 and November 2004 at five localities in the Atlantic Forest of Misiones Province, Argentina. The localities were: Parque Nacional Iguazú (25° 41' S, 54° 27' W), a colony near Iguazú International Airport (25° 43' S, 54° 29' W), the town of Puerto Iguazú (25° 36' S, 54° 34' W), Parque Provincial Urugua-i (25° 52' S, 54° 11' W), and Parque Provincial Esmeralda (25° 53' S, 53° 53' W). These colonies contained 16 to 104 nests. Only a few nests at each colony (10–20%) were <5 m above ground level and most could be inspected without unduly stretching or damaging the structures. Inspected nests were close (4–70 cm) to other nests, and built in the main trees of each colony.

I observed and recorded cacique and cowbird behavior around the eight colonies during 130 hrs with 8 x 42 binoculars and tape recorders. Both Red-rumped Caciques and Giant Cowbirds are sexually dimorphic in size, iris color, and plumage brightness (Jaramillo and Burke 1999, pers. obs.). Red-rumped Caciques in Argentina and nearby Brazil are considerably smaller (males 93 g, females 66 g) than Giant Cowbirds (males 209 g, females 122 g) (Contreras 1983, Belton 1985, Darien and Camperi 1994; specimen at Burke Museum, University of Washington, Seattle, USA). Digital micro-cameras were placed in some cacique nests containing nestlings in November 1996, by a crew producing a documentary film for Japanese National Television (NHK).

Nests were found during both egg-laying and incubation periods (“egg stage”), and with at least one hatched host or parasite nestling (“nestling stage”). Nests were examined on 2–4 different days, until failure, hatching or fledging. People living near the colonies also informed me on nest contents, fledging dates, and predation events. Estimated laying dates for Red-rumped Cacique eggs that hatched are based on the incubation period of 18 days reported by Duca and Marini (2004). Eggs were numbered with waterproof ink, and their maximum length and width was measured with digital calipers to the nearest 0.1 mm. I estimated egg volume with the formula 0.524 × l × w², where l and w were the egg maximum length and width (Preston 1974). Nestlings were described and photographed, and I obtained their bill measurements with digital calipers. Body mass of nestlings was measured with Pesola scales accurate to 0.5 g. Small nestlings were marked with waterproof ink and afterwards color bands. Host and parasite fledgling success are compared by using ratios of fledglings/eggs. I used Statistica 5 (StatSoft, Tulsa, Oklahoma, USA) for statistical analysis.

RESULTS

Breeding.—Red-rumped Caciques breed in Misiones Province and northeastern Corrientes Province within Argentina. Misiones colonies (n = 68) contained from seven to 104 nests at times spread over up to three neighboring trees; Corrientes colonies (n = 14) contained nine to 30 nests. The southernmost Argentinean colony was observed at Paso de los Libres (29° 41' S. 57° 04' W), Corrientes. I did not find Giant Cowbirds at this site in 1995, but A. A. Bodrati (pers. comm.) saw three individuals 50 km north of this site in 2007. Other colonial nesting cacique or oropendola were not observed nesting in this area.

The eight studied colonies were in man-made clearings, near houses, barns, and other buildings and, when tolerated by people, were reused during many years. I did not observe nests of aggressive wasps in the colony trees. Nesting activities were quite asynchronous in the larger colonies. The start of the cacique breeding season varied between years during my study, even at the same locality. Active colonies with a few incubating females were seen in the Iguazú area by mid-June 1996 but, in the colder winter of 1997, nests were still unfinished at the end of August. Egg-laying continued at least until 21 December. Postbreeding cacique flocks with dependent fledglings occurred in December–March along trails in...
The eggs were pale buff, marked and unmarked (39 of 46, 85%). The parasitized with one cowbird egg. Cowbird eggs occurred in 27 of 38 cacique nests (mean = 0.47). Earlier dates are possible; the June-July cacique 18 eggs). Most nests (17 of 27, 63%) were localized around a nest or a group of nests. 

Cowbird groups landed first at the highest branches of colony trees, but afterwards cowbird females visited nests above and below 5 m. Male cowbirds made short calls, but single females were silent on visits. Caciques reacted to visiting cowbirds with loud and rasping alarm calls, but the volume of colony noise was lower than in the presence of raptors or other nest predators. Male caciques attacked and chased cowbirds perched anywhere in the colony tree, but female attacks were usually localized around a nest or a group of nests.

Extreme egg-laying dates for nine Giant Cowbirds were 16 September and 20 December. Earlier dates are possible; the June-July cacique nests of 1996 were too high to be examined, but cowbirds were seen near those colonies.

**Parasitism During the Egg Stage.**—I did not observe host eggs in three dump nests containing 5, 5, and 6 cowbird eggs, and the nests appeared abandoned during all visits (eggs cold, no females present). These dump nests had little lining material, which suggests that desertion may have occurred prior to host egg laying. The maximum number of host eggs observed in the remaining 24 parasitized nests was two eggs (6 nests), one egg (16 nests), and zero eggs (2 nests) with a mean of 1.13 cacique eggs. Two-egg host clutches were significantly more frequent in non-parasitized nests (10/11) than in those containing cowbird eggs (6/24) (z² = 13.20, df = 1, P < 0.001). Cracked or crushed host eggs (n = 4) were observed in six parasitized clutches. Three cracked or crushed parasite eggs were also observed in nests with five and six cowbird eggs. I did not observe caciques or cowbirds damaging or removing eggs.

**Host and Parasite Nestlings.**—Only five of 14 nests (35.7%) found in the nestling stage had eggs or nestlings of Giant Cowbirds. Nest contents for this entire sample were 20 host nestlings, two cowbird nestlings, one host egg, and three cowbird eggs. None of the four eggs hatched. The incubation period for one Giant Cowbird egg was estimated at 12-13 days.

Host and parasite nestlings differed in appearance and size. Feathered host nestlings had visible red rumps, bills with a small frontal casque colored pale yellowish gray, pale yellow flanges, and brownish eyes with bluish reflections. The three feathered cowbird nestlings had uniform blackish plumage, pinkish-ivory colored bills, yellow flanges, and conspicuous pinkish-ivory frontal casques edged with pale yellow. The eyes were dark brown and surrounded by a triangular facial patch of bare flesh-colored skin. The total length of the frontal shield plus bill was 23 mm for a partially feathered cowbird nestling at 12 days of age; the equivalent length was
19.7 mm for a cacique nesting of the same age. Cowbird nestlings (n = 3) attained 90-130 g in body mass at days 12-15, while host nestlings fledged with body masses of 67 to 85 g (n = 14). Female Red-rumped Caciques in Misiones frequently reared broods of two host nestlings. However, the three cowbird nestlings were reared alone, as the host eggs remaining in the three nests did not hatch (2 cases), or the host chick died and was probably removed by the host female.

Behavior of host and parasite nestlings during provisioning episodes (in 2 nests observed with the micro cameras) had parallel development. Nestlings during the first week were rather passive, often subject to brooding, and gaped at feeding females from the bottom of the nest. Nest-shaking caused by the incoming host female stimulated older nestlings of both species to climb the nest walls towards the entrance, gaping with stretched necks. Host and parasite nestlings in the last days of the nesting stage remained perched near the entrance most of the day with their bills outside the nest and clearly visible with binoculars. Bills of cowbird nestlings were larger and paler than those of host nestlings. The nesting period of one fledged cowbird was estimated to be 18 days.

Botflies (Philornis spp.) infested seven host nestlings and one cowbird nestling. Eight botfly larvae were observed on a cowbird nestling at 4 days of age with a body mass of 41.5 g; 6 days later the number of visible larvae had increased to 19 and nestling body mass had increased to 51 g. One non-infested cowbird nestling had a mass of 71 g at day 9. Another cowbird nestling was infested with botflies prior to this study in one of my colonies (Jorge Anfuso and Silvia Elsegood, pers. comm.). Infested host nestlings (n = 7) had only 7-9 Philornis larvae, and no mortality or abnormal growth was detected.

Reproductive Success of Host and Parasite.—
Data are presented only for the 35 nests found in the egg stage. Precise estimates of success were difficult as fledglings moved into dense forest cover within 12 hrs of leaving the nest. The 35 nests contained 67 cacique eggs, which produced a minimum of 11 fledglings (16.4%). The estimate is slightly increased to 11 fledglings from 61 eggs (18%) if the three dump nests did not contain host eggs. Only one of the 46 cowbird eggs (2.2%) was known to produce a fledgling.

Monkeys were not seen in the man-made clearings used for nesting, and the main nest predators of cacique colonies were three toucan species: Toco Toucan (Ramphastos toco), Gren-billed Toucan (R. dicolorus), and Chestnut-eared Aracari (Pteroglossus castanotis). I saw two Toco Toucan raids destroying a colony of 16 nests, part of which were witnessed similar cases, and several predation sequences were filmed by the NTB documentalists. A. A. Bodrati (pers. comm.) also observed Saffron Toucanet (P. bailloni) predation of cacique colonies in Misiones. Strong rainstorms knocked down several nests, affecting host and parasite success. Specific causes of hatching failure for Giant Cowbird eggs included egg dumping (3 nests with 16 eggs), and poor synchronization with the host's egg laying. At least three cowbird eggs were laid 6-8 days before the host eggs hatched, i.e., 10-12 days after the start of incubation. Those eggs remained in the nest but did not hatch.

DISCUSSION

Many aspects of the breeding biology of Red-rumped Caciques (including breeding season, nests, clutch size, egg coloration) agree with information obtained in eastern Brazil (Duca and Marini 2004, 2008; Pizzi 2009). Important exceptions were larger colony sizes in Misiones and brood parasitism by the Giant Cowbird, which is rare or absent in large areas of eastern Brazil (Jaramillo and Burke 1999).

The incidence of parasitism of Red-rumped Caciques is among the highest reported for Giant Cowbirds; Fleischer and Smith (1992) reported a 54.2% incidence for Yellow-rumped Caciques in Panama. Cowbirds were far less numerous than caciques in Misiones, and the 71% incidence of parasitism suggests high egg productivity of female parasites, as for other cowbirds (Scott and Ankney 1983). Clutches parasitized with two or more eggs were 37% in my sample, almost identical to the 37.5% reported for Yellow-rumped Caciques in Panama (Fleischer and Smith 1992).

Mean measurements of Giant Cowbird eggs from northeastern Argentina were similar to those reported from Panama (35.8 × 24.9 mm) (Fleischer and Smith 1992) and Suriname (34.0 × 25.5 mm) (Haverschmidt 1966, 1967), indicating considerable uniformity in size throughout an extensive geographic range. Variation in egg color is important. White unmarked eggs, the most common morph in northeastern Argentina, occur less commonly in Panama (Fleischer and Smith 1992), Costa Rica (Crandall 1914), and Venezuela.
In Particular, the pale-colored casque occurs in structures in nestlings of most oropendola species. However and Post (1999), but resembles similar nestlings (Fraga 1979; Lowther 1993, 1995; Johnson and Lanyon 1999); this similarity may have evolved through mimicry. Cowbird nestlings gives some resemblance to host flings. A pale bill is found in nestlings of the Giant Cowbird and Red-rumped Cacique nestlings. The resemblance between M. rufoaxillaris ("Creaming Cowbird") (Fraga 1979) and human experience. The pale bill of Giant Cowbirds reported here seems surprisingly low for a specialized brood parasite. However, my data on contents of nests found with nestlings suggest a ratio of 10 host young for each cowbird young. I observed one Giant Cowbird fledgling in seven postbreeding cacique flocks in Misiones, which included 30+ host fledglings.

Crandall (1914) first described two Giant Cowbird young from nests of Montezuma Oropendolas in Costa Rica, broadly agreeing with my findings. However, he did not mention the existence of a conspicuous pale frontal casque, and found no resemblance between host and parasite nestlings. The resemblance between Giant Cowbird and Red-rumped Cacique nestlings is slight in my experience. The pale bill of Giant Cowbird nestlings gives some resemblance to host nestlings. A pale bill is found in nestlings of the Screaming Cowbird (M. rufoaxillaris) (Fraga 1979), a species ancestral to Giant Cowbirds (Johnson and Lanyon 1999); this similarity may have not evolved through mimicry.

The conspicuous pale frontal casque of Giant Cowbird nestlings is unique among cowbird nestlings (Fraga 1979; Lowther 1993, 1995; Lowther and Post 1999), but resembles similar structures in nestlings of most oropendola species. In particular, the pale-colored casque occurs in young Crested Oropendolas (Psarocolius decumanus), a common host of the Giant Cowbird (Goeldi 1894, Guimarães 1926, Schäffer 1957). This casque is retained in adult Giant Cowbirds (Webster 2003), but becomes relatively small, black-colored, and partially covered by plumage. Webster (2003) also noticed an elongated skull in adult Giant Cowbirds, and those of oropendolas and caciques. His suggestion that Giant Cowbirds could be related to caciques and oropendolas and not to other cowbirds is clearly contradicted by DNA data (Lanyon 1992, Johnson and Lanyon 1999). Mimicry is a plausible explanation for the general resemblance between the head parts of nestling Giant Cowbirds and oropendolas.

Mutualism between Giant Cowbirds and their hosts reported by Smith (1968, 1980) in Panama is not supported by Argentinian data. First, nestling Giant Cowbirds were infested by Philornis larvae. Second, Giant Cowbird nestlings in my sample could not preen host nestlings because they were reared alone. This situation may arise from the large disparity in body mass between host and parasite nestlings. Third, cacique nestlings survived light Philornis infestations, as reported for other Misiones passerines (Cockle and Bodrati 2009). Last, nesting Red-rumped Caciques were aggressive to visiting Giant Cowbirds. My results agree with studies from Peru and Costa Rica (Robinson 1988, Webster 1994) in indicating a negative effect of Giant Cowbird parasitism.

ACKNOWLEDGMENTS

The crew of Nippon Hōso Kyōkai (NHK) documentalists (particularly Kenji Mori) started my interest in this study. Parques Nacionales (Argentina) and the Ministerio de Ecología (Misiones) provided the required permits. Many park rangers in Misiones (national and provincial), and Andrés Bosso and Lucio Aspero, helped my work or provided important information. I am particularly thankful to Jorge Anfuso and Silvia Elsengard for allowing me to study caciques around their house, and for gathering information on many aspects of this study. A. A. Bodrati and K. L. Cockle helped me in many ways, particularly at Esmeralda. Sharon Birks provided information on a specimen at the Burke Museum. The manuscript was improved by comments from A. A. Bodrati, K. L. Cockle, and J. I. Areta.

LITERATURE CITED

GOELDI, E. A. 1894. As aves do Brazil. Livraria Clasica Alves, Rio de Janeiro, Brazil.
ALTITUDINAL VARIATION IN PARENTAL PROVISIONING OF NESTLING VARIED TITS (POECILE VARIUS)

JONG KOO LEE,1 OK-SIK CHUNG,1,2 AND WOO-SHIN LEE1

ABSTRACT.—We recorded parental provisioning rates of Varied Tits (Poecile various) at different altitudes (n = 17, 7, and 11 nest boxes at 300, 900, and 1,400 m, respectively) to examine if males and females cooperate in response to increased provisioning pressure due to nutritional demands of nestlings. Females provisioned nestlings more than males irrespective of altitude. Provisioning rates of males and females tended to increase with elevation, but the increase was greater for males. Provisioning was low early in the nestling period, and gradually increased reaching a peak between 9 and 10 days after hatching. The provisioning rate of females at the peak provisioning period (8–10 days) did not increase markedly at any altitude. Provisioning by males during the peak period increased and they contributed more during this period than at other times. The provisioning rate of males increased linearly with elevation. The provisioning rate of female Varied Tits also increased with elevation, but the increment ratio was lower than that of males. Changes in provisioning rates with elevation may be due to the need to invest more in parental care under unfavorable environmental conditions. Parents at high altitudes experience more difficulty provisioning, not only because of nestling growth, but also because provisioning is required more often. Thus, increased provisioning by males, which have a lower provisioning frequency relative to females, may be an investment to reduce foraging pressure on females and to ensure survival of nestlings.

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Newly-hatched birds depend completely on their parents for food. Thus, parental provisioning has a crucial role in survival of young (Bengtsson and Rydéén 1983, Keller and Van Noordwijk 1994, Wright et al. 1998). Parents rapidly adapt to changes in the environment by altering their provisioning rates and through cooperation with partners (Wright and Cuthill 1989, Davies 1991). Increases in provisioning rates can improve survival of nestlings, but parents may be at risk of starvation and predation (Eggers et al. 2005). Sauss et al. (2005) reported higher costs were incurred because of increased flying distance and provisioning frequency. Provisioning is a burden for females and, during the nestling period, mass loss incurred by the female parent is linearly related to provisioning frequency (Nur 1984a, b). This indicates it is necessary for females to achieve trade-offs between their energy costs and benefits for nestlings (Badyaev and Ghalambor 2001). Thus, it is important to examine if provisioning frequency can be increased with minimal energy expenditure. Others have found provisioning rate can change due to habitat quality, prey population density, prey size, and food availability (Nour et al. 1998; Grieco 2002; Tremblay et al. 2003, 2005). Provisioning rate is also affected by gender of parents because sexual strategy and roles in nestling care differs (Kuitunen et al. 1996, Rytkonen et al. 1996, Grieco 2001, Quillfeldt et al. 2005).

Altitude contributes to environmental gradients and influences the ethology, morphology, and ecology of reproduction of a species. The ecology of reproduction of birds at high altitudes is considerably different from those at low altitudes, even of the same species (Cody 1966, Boyce 1979, Badyaev 1997). Provisioning frequency of birds, in particular, increases at higher altitude because of environmental differences resulting from elevation (Badyaev and Ghalambor 2001). Parents at high altitudes experience more difficulty provisioning, not only due to nestling growth (Wittenberger 1982), but also because feeding is required more often (Badyaev and Ghalambor 2001). Consequently, birds at high altitude have a greater challenge of reaching a trade-off between survival and reproduction than those breeding at low altitudes and strategies may reflect their gender.

Varied Tits (Poecile various) are primarily resident and are distributed across Korea, Japan, and parts of China. Their habitats range from low to high mountains; they are socially monogamous and raise their young together (Yamaguchi and Kawano 2001). Thus, they are an appropriate species for study to examine the contribution of females and males in provisioning their young under the restriction of elevation.

Our objectives were to examine: (1) provisioning rates of Varied Tits at different altitudes, and (2) how males and females respond and cooperate
TABLE 1. Longitude/latitude and brood size of Varied Tits at three sites, Mt. Jiri, Korea, 2007.

<table>
<thead>
<tr>
<th>Area</th>
<th>Longitude/latitude (mean ± SE (n))</th>
<th>Brood size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piagol (300 m)</td>
<td>N 35° 15' 37.1&quot; E 127° 35' 00.1&quot;</td>
<td>6.69 ± 0.75 (17)</td>
</tr>
<tr>
<td>Siamjae (900 m)</td>
<td>N 35° 18' 14.6&quot; E 127° 20' 46.6&quot;</td>
<td>6.26 ± 1.15 (7)</td>
</tr>
<tr>
<td>Nogodan (1,400 m)</td>
<td>N 35° 17' 36.9&quot; E 127° 31' 42.4&quot;</td>
<td>5.90 ± 0.70 (11)</td>
</tr>
</tbody>
</table>

under increased provisioning pressure caused by elevation and growth of nestlings.

METHODS

We selected three areas (Piagol at 300 m, Siamjae at 900 m, and Nogodan at 1,400 m) with similar vegetation but at different altitudes along Mt. Jiri at the southern extremity of Korea and established 48 nest boxes at each site in November 2006. This research was conducted during the breeding season (Apr-Jun) of Varied Tits in 2007. Parents were captured at their nest boxes while incubating. A small amount of blood was collected from each bird to ascertain gender genetically using an amplification refractory mutation system method (Ito et al. 2003), and a colored band was placed on legs of females to distinguish them from males. Video cameras (Sony Handycam HDR-SR1) were positioned in front of nest boxes in which the gender of parents was known, and visits (per hour) of female and male Varied Tits were recorded. We acquired data from 17 nests at Piagol, 7 nests at Siamjae, and 11 nests at Nogodan; the recording time for each nest was 4-8 hrs per day. The total recording time was 1,204, 571, and 976 hrs for the three areas, respectively. The provisioning rate of males or females was calculated as the number of times the parent visited the nest per hour divided by the number of nestlings in the nest. We used repeated measure analysis of variance (ANOVA) to test effects of nesting age on effects of gender of parents and sites.

RESULTS

Brood size decreased with altitude (Table 1). The provisioning rate of female Varied Tits was higher than for males in all three areas (Fig. 1, Table 2). Provisioning rates increased with altitude based on significant differences among the three areas (Fig. 2, Table 3). The provisioning rate of parents based on nestling age was low during the first few days after hatching, but gradually increased and reached a peak when nestlings were 10 days of age (Pearson Correlation = 0.673, P < 0.0001). Provisioning rates of females during the peak provisioning period (8-10 days) were not significantly different from those at other times of the nesting period at any of the three sites (Table 3). However, provisioning rates of males during this period were different from those at any other time (t-test, P < 0.0001). The provisioning rate of female Varied Tits increased with elevation (Table 3), because variation in provisioning rates across the altitudinal gradient was higher for males than for females (repeated measure ANOVA, Site*gender, P = 0.001). The increment ratio of males provisioning rate to female provisioning rate increased at Siamjae (900 m) and Nogodan (1,400 m) until 9-10 days after hatching.
TABLE 2. Differences in provisioning rate of male and female Varied Tits at three sites, Mt. Jiri, Korea, 2007 (Repeated measure ANOVA within nestling age).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Site</th>
<th>Between</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provisioning rate</td>
<td>Piagol (300 m)</td>
<td>Male and Female</td>
<td>1</td>
<td>185.54</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td></td>
<td>Siamjae (900 m)</td>
<td></td>
<td></td>
<td>143.32</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td></td>
<td>Nogodan (1,400 m)</td>
<td></td>
<td></td>
<td>79.33</td>
<td>&lt;0.001**</td>
</tr>
</tbody>
</table>

** = significant (P < 0.05).

hatching, as there was a strong positive correlation between the ratio and the number of days (until 9-10 days) after hatching (Table 4). The tendency of increase in the provisioning rate until 9-10 days of the nestling period was higher for males than for females. The relative ratio of male provisioning rate to that of females at Piagol (300 m) tended to increase, but the increase was not statistically significant.

DISCUSSION

The provisioning rate of males and females increased with elevation for Varied Tits (Fig. 1) and this behavior seems to be essential to producing offspring under challenging environmental conditions. Habitat quality in mountainous regions with elevation gradients is influenced strongly by elevation because of habitat condi-

![FIG. 2. Provisioning rate of male and female Varied Tits, Mt. Jiri, Korea, 2007. (A) Both parents, (B) Males, (C) Females.](image)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Between</th>
<th>Within</th>
<th>Gender</th>
<th>Period</th>
<th>df</th>
<th>( p )</th>
<th>Post-hoc (Tukey)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provisioning rate</td>
<td>Sites</td>
<td>Nestling age</td>
<td>Male</td>
<td>All</td>
<td>2</td>
<td>&lt;0.001</td>
<td>Pi-Si &lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>2</td>
<td>&lt;0.001</td>
<td>Si-No &lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>2</td>
<td>&lt;0.001</td>
<td>Pi-No &lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>All</td>
<td>0.001</td>
<td>Pi-Si</td>
<td>0.005 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>All</td>
<td>0.001</td>
<td>Pi-No</td>
<td>&lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>All</td>
<td>0.001</td>
<td>Si-No</td>
<td>&lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Female</td>
<td>All</td>
<td>0.001</td>
<td>Pi-No</td>
<td>&lt;0.001 **</td>
</tr>
<tr>
<td>Peak (day 8–10)</td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>0.676</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>&lt;0.001</td>
<td>Pi-Si</td>
<td>&lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>&lt;0.001</td>
<td>Si-No</td>
<td>&lt;0.001 **</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>All</td>
<td>&lt;0.001</td>
<td>Pi-No</td>
<td>&lt;0.001 **</td>
</tr>
</tbody>
</table>

* Pi = Piagol (300 m), Si = Siainjae (900 m), No = Nogodan (1,400 m).

TABLE 4. Relative rates of male to female provisioning (provisioning rate of male/to that of female) by age of nestlings, Mt. Jiri, Korea, 2007.

<table>
<thead>
<tr>
<th>Period</th>
<th>Pearson Correlation Coefficient</th>
<th>( p )</th>
<th>(^*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piagol</td>
<td>Until day 10</td>
<td>0.21</td>
<td>0.5546</td>
</tr>
<tr>
<td>Siainjae</td>
<td></td>
<td>0.67</td>
<td>0.0320</td>
</tr>
<tr>
<td>Nogodan</td>
<td></td>
<td>0.70</td>
<td>0.0500</td>
</tr>
</tbody>
</table>

* ns = not significant, ** = significant (\( p < 0.05 \)).

It is known that relative nestling demand across avian species is larger at higher altitude because of cold temperature, rapid seasonality, and fluctuation in food availability which results in increased parental effort in provisioning (Badyaev and Ghalambor 2001). This increasing parental effort appears to be critical for survival of offspring, especially at higher elevation (Badyaev 1997, Blackenhorn 1997). We did not include other factors believed to affect provisioning rate such as habitat quality, prey population density, prey size, and food availability in our analysis (Nour et al. 1998; Tremblay et al. 2003, 2005). We assume our results that parental provisioning rate increased with elevation indicated that altitude did reflect the effect of those factors.

The provisioning rate of females was not different from that at other times in the peak provisioning period (from 8 to 10 days after hatching); males, in contrast, were considerably different during this period (Fig. 2, Table 3). Females had a higher provisioning rate than males and had the greater burden of provisioning nestlings. Males appeared to increase their provisioning rates to reduce the cumulative pressure on females of increased provisioning and elevation restrictions. Males at high altitude may compensate for reduced fecundity by increasing their breeding effort (Badyaev 1997, Badyaev and Ghalambor 2001). The peak provisioning period is the most nutritionally demanding for nestlings (Gowaty 1983) and, it is assumed that by increasing their provisioning rate, males help compensate for the female's threshold level of provisioning to increase the survival rate of nestlings.

Monogamous males tend to provide more investment in raising a brood (Krebs and Davies 1993). However, there are interspecific differences in the extent and type of cooperation monogamous males provide to their mates (Beer 1983, Coulsen and Wooller 1976). Female Varied Tits in our study were the main suppliers of food, but the relative ratio of male to female provisioning rates increased steadily until it reached a peak at 10 days at the study sites, except at Piagol (Table 4). Female and male provisioning rates did not equally increase as a brooding progressed, as the provisioning rate of males increased more than that of females. The male's provisioning role gradually increased until 9–10 days of nestling age. Females have a higher provisioning frequency relative to males, but it is more difficult for females to increase provisioning frequency. Thus, when males increase provisioning more dramatically in response to the increase in nutritional demand of nestlings seems to be essential for females and for the benefit of nestlings. Thus, parents can increase their provisioning frequency during short periods, but cannot maintain increased provisioning frequency for a long period (Leffelaar and Rovertson 1986). This strategy has a significant impact on the potential survival of
nestlings as well as for females (Gowaty 1983). Successful breeding at high elevations depends on male care (Lyon et al. 1987, Badyaev 1993). Grudel (1987) reported similar strategies, in which the provisioning rate of males increased when brood size was larger, but there was no change in the provisioning rate of females if brood size was smaller. Royama (1966) showed the relative provisioning rate of females decreased if brood size was smaller. Staus et al. (2005) reported the provisioning rate and the flight distance for foraging increased under unfavorable conditions. These results suggest provisioning rates depend on foraging conditions and energy demands of nestlings.

Altitude appears to be an environment factor that influences several variables such as prey quality and quantity, breeding timing, temperature, etc., but we do not know which variables change with altitude to directly affect changes in provisioning rates. Further research is needed to identify the causes of change in provisioning activities considering energy benefits and cost to parents.

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LITERATURE CITED


AVIFAUNA OF THE GRAN PAJONAL AND SOUTHERN CERROS DEL SIRA, PERU

MICHAEL G. HARVEY,1,2,6 BENJAMIN M. WINGER,1,3,4 GLENN F. SEEHOLZER,1,2 AND DANIEL CACERES A1

ABSTRACT.—Field surveys conducted between 4 September and 17 November 2008 resulted in the first comprehensive inventory of the avifauna of the outlying highlands of the Gran Pajonal and southern Cerros del Sira in central Peru. We report 462 bird species representing 52 families from above 900 m elevation. We describe the avian communities of humid montane habitats and savanna, and provide accounts for 22 species for which we obtained either new distributional data or information of taxonomic significance. We also discuss avian migration, reproduction, molt, and conservation in the region. Our results highlight the richness and uniqueness of the avifauna of the Cerros del Sira and Gran Pajonal, and reinforce the scientific and conservation importance of the eastern Andes and its outlying ridges. Received 21 April 2010. Accepted 14 December 2010.

The complex topography, geology, and climate of the Peruvian Andes have produced isolated patches of habitat with unique avian communities and distinct taxa (Terborgh and Weske 1975, Fitzpatrick 1977, O'Neill et al. 2000), many of which are only beginning to undergo ornithological exploration (Schulenberg and Awbrey 1997, Schulenberg et al. 2001). The Cerros del Sira (henceforth Sira) and Gran Pajonal in the departments of Huánuco, Pasco, Junín, and Ucayali in central Peru comprise a highland area of 12,000 km² to the east of the high Andes. The Sira and Gran Pajonal are notable for the presence of isolated patches of montane evergreen forest, defined as forest in areas where clouds regularly touch the mountains (Stotz et al. 1996), and savanna, or areas of grass and shrubs locally referred to as "pijnones" (Chrostowski and Denevan 1970). Montane evergreen forest in the upper elevations of the Sira is isolated from similar habitat in the main Andes by 100 km (Terborgh and Weske 1975). The savannas of the Gran Pajonal are isolated from the nearest large contiguous block of savanna in Bolivia by >600 km, although small areas of savanna and seasonally dry forest occur in dry valleys of the eastern Andes of Peru and Bolivia (Scott 1977, Linares-Palomino 2006, Pennington et al. 2006).

Previous ornithological work conducted in the Sira was concentrated at its northern edge (Weske and Terborgh 1971, Terborgh and Weske 1975, Weske and Terborgh 1977, Terborgh 1985, Graves and Weske 1987, Mee et al. 2002). The only available information on the birds of the southern Sira and Gran Pajonal is from a small collection made near the village of Tsiioventeni by personnel from Andrew’s University (Thoresen 1974; T. S. Schulenberg, pers. comm.). The savannas of the Gran Pajonal have not received any ornithological attention, despite their status as a prominent example of a rare biotope in Peru.

We present the results of the first intensive ornithological inventory of the Gran Pajonal and southern Cerros del Sira. We provide descriptions of the bird communities in the savanna and humid montane habitats, as well as details on the status of select species of interest. We also comment on boreal and austral migratory species, reproductive behavior, molt, and the biogeographic and conservation implications of our results. A species list annotated with distribution, abundance, elevation, and habitat information and incorporating data from previous work in the region is presented in the Appendix.

STUDY AREA AND METHODS

Geography.—The Cerros del Sira and Gran Pajonal form an upland region bordered to the west and north by the valley of the Pachitea River, to the east by the valley of the Ucayali River, and
to the south by the valleys of the Tambo and Peréné rivers (Fig. 1). The Cerros del Sira form a linear ridge extending 250 km roughly NNW to SSE, and located >100 km east of similar elevations in the Andes. The crest of the ridge is generally 1,300–1,700 m in elevation but in places exceeds 2,200 m. The ridge of the Sira is interrupted in two locations: a low (~1,000 m) saddle bisecting the range at 09° 45′ S, and the valley of the Unine River at 10° 54′ S. The spine of the Sira on the eastern slope is characterized for much of its length by a sheer cliff face intersected perpendicularly by steep ridges and valleys that descend east to the Ucayali River. The western slope of the Sira descends relatively gradually and, at the southern end, levels into a plateau that averages ~1,200 m in elevation and extends 50 km to the west at its widest. This plateau is locally referred to as the Gran Pajonal, after the patches of savanna ("pajonales") scattered over its surface, and retains a tenacious connection to the foothills of the Andes through a series of articulated ridges dividing the Chanchamayo and Pachitea valleys. Human population densities are low in the region surveyed and consist almost entirely of titled Ashéninka indigenous communities, except for a colonist settlement at Oventeni (Hvalkof 1998).

Climate.—A government report (ONERN 1968) provides general climatological data for the region. The climate of the Cerros del Sira and Gran Pajonal is classified as humid subtropical. Monthly mean high temperatures at Oventeni in the Gran Pajonal range from 28.3° to 30.1° C, and monthly mean low temperatures from 11.2 to 17.8° C. Rainfall at Oventeni averages a moderate 2,166 mm annually and is concentrated between November and April. Weather data from the higher elevations of the Cerros del Sira are unavailable, but temperatures likely average lower
TABLE 1. Sampling effort in 2008 at primary study sites in the Gran Pajonal and southern Cerros del Sira, Peru. Habitat codes are in the Appendix.

<table>
<thead>
<tr>
<th>Habitats surveyed</th>
<th>Dates surveyed</th>
<th>Observer-hrs</th>
<th>Net-hrs</th>
<th>Species detected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monte Tabor</td>
<td>Sp,F,F,F₁</td>
<td>6-11 Sep</td>
<td>303</td>
<td>92</td>
</tr>
<tr>
<td>Oventeni</td>
<td>Sp,F,F₁,F₂,M</td>
<td>4-6, 12-15, 17-19 Sep</td>
<td>307</td>
<td>12</td>
</tr>
<tr>
<td>Menkoremon</td>
<td>P₁,F₁</td>
<td>2, 4-6 Oct</td>
<td>194</td>
<td>0</td>
</tr>
<tr>
<td>Upper Shaani Valley</td>
<td>F₁</td>
<td>23 Sep-1 Oct, 3, 8-9 Oct</td>
<td>474</td>
<td>290</td>
</tr>
<tr>
<td>Upper Sinipo Valley</td>
<td>F₁</td>
<td>1-6 Nov</td>
<td>282</td>
<td>83</td>
</tr>
</tbody>
</table>

and precipitation higher due to the deposition of rain by warm, moist winds from the east. At least short periods of heavy rainfall occurred on a nearly daily basis during our study, and prolonged downpours were common. Atalaya, at the eastern foot of the southern Sira, averages 2,950 mm of precipitation annually.

Geology and Soils.—Soils in the region are largely derived from residual material from upland formations with some alluvial deposits. Most pajonales overlay calcareous shale bedrock with soils comprised of poorly draining red latosols or yellow podzolics (Scott 1978). The montane forests of the Sira ridge occur chiefly on lithosols derived from red Permian sandstones (Chrostowski and Denevan 1970, Scott 1978), which are relatively poor in nutrients and support a thin organic cap at higher elevations (ONERN 1968). Patches of fine, white substrates of unknown composition occur sporadically in humid forest in the highlands (pers. obs.). Rain water in these locations often collects at the surface, suggesting low internal drainage.

Vegetation.—The Gran Pajonal plateau (800-1,300 m) is covered in humid evergreen forest interrupted by pajonales; these are generally smaller (<100 ha) and total 9,000-10,000 ha region-wide, 3% of the total area of the Gran Pajonal (Hvalkof 2006). The historical and floristic relationships between the pajonales of the Gran Pajonal and other neotropical savannas and seasonally dry forest remain unclear (Linareς-Palomino 2006). Climatic and edaphic factors may have contributed to their origins, but the pajonales have been deliberately maintained through fire management by the indigenous Ashéninka population for centuries (Chrostowski and Denevan 1970; Scott 1977, 1978; Hvalkof 1998, 2006). Several failed national cattle-raisin efforts in the Gran Pajonal since the 18th century have augmented the extent of open areas and, in recent years, settlers have increased deforestation for pastoral and agricultural uses (Hvalkof 2006). Forest is much more widespread regionally, but its characterization is complicated by the slow transition between tropical lowland evergreen forest in the valleys and montane evergreen forest on the ridges of the Cerros del Sira. The crests of the highest ridges of the Sira support elfin forest, semi-humid/humid montane scrub, and a habitat resembling paramo grassland. Additional important avian habitats scattered throughout the region include Chusquea bamboo, small marshes, and rivers and streams. Our habitat descriptions generally follow Stotz et al. (1996); however we follow Grubb (1974) in distinguishing between lower montane evergreen forest, which is dominated by trees with mesophyll leaf types and vascular epiphytes, and upper montane forest with more microphyllous trees and bryophytic epiphytes. We also erect a separate category for the pajonales, although some may be within the broader category of semi-humid/humid montane scrubs.

Study Sites.—The authors surveyed the Gran Pajonal and southern Cerros del Sira during 38 days between 4 September and 17 November 2008, focusing on pajonales and montane evergreen forest at five sites (Table 1).

Monte Tabor (10° 53’ S, 74° 11’ W) is a sandstone cap at 1,350 m at the northern edge of Quitchungari Ridge with forested slopes and a 175 ha pajonal at its crest (Scott 1978). The vegetation of the Monte Tabor pajonal is a short, windswept community of grasses dominated by Tricachne spp., Aristida spp., and Vernonia spp. (Scott 1978) with occasional small islands of trees and shrubs, and sparse coverage in areas by bracken fern (Pteridium spp.). The pajonal boundary is characterized by an abrupt demarcation with surrounding forest. No agriculture or grazing currently occurs on the Monte Tabor pajonal, but local Ashéninka villagers regularly burn it, and it was historically the site of a mission
The Shinipo Valley (10° 31' S, 74° 07' W) is on the eastern slope of the Cerros del Sira and includes elevations between 900 and 1,200 m where the dominant habitat is upper montane evergreen forest. Most forest patches around Oventeni are second growth, although some primary remnants may persist (Scott 1978).

The Shaani Valley site (10° 42' S, 74° 07' W) is on the upper slopes of the saddle between the Sira ridge and the isolated peak of Menkoremon. This site includes elevations between 1,800 and 1,900 m where the dominant habitat is upper montane evergreen forest. Patches of bamboo (Chusquea spp.) are frequent in this area, and mosses and epiphytes are abundant. Also present on patches of fine white substrates is a stunted forest containing numerous palms (Arecaceae) and other plants with thick, glossy leaves.

Menkoremon (10° 42' S, 74° 06' W) is the highest summit in the southern Cerros del Sira at 2,240 m and is covered in elfin forest transitioning to a plant community resembling paramo grasslands. The latter is dominated by grasses, but also includes scattered ground bromeliads (Bromeliaceae) and Paepalanthus spp., heather (Bejaria aestuans), orchids (Orchidaceae), ferns (Lygodium spp., Sticherus spp., Gleichenia spp.), and club mosses (Lycopodiella spp.). We photographed Drosera spp. (Droseraceae), a seer genus in Peru, and one that is indicative of nutrient-depleted soil (Rodulfo Vásquez, pers. comm.).

The Shinipo Valley (10° 31' S, 74° 07' W) is on the eastern slope of the Cerros del Sira and includes elevations between 900 and 1,200 m. The habitat is lower montane evergreen forest with a canopy height of ~30 m on the slopes and as low as 10 m on ridge crests.

We also recorded observations briefly or opportunistically at three secondary localities: Santeni Valley (10° 42' S, 74° 09' W), Timpani Valley (10° 40' S, 74° 05' W), and Cerro Quitchungari (11° 03' S, 74° 11' W; Fig. 1).

Field Methods.—We conducted surveys across all habitat types at each primary site (Table 1). Observational surveys were conducted along transects that followed trails or water courses between 0500 and 1200 hrs PET and again between 1400 and 1830 hrs. Observation data have been deposited in the Avian Knowledge Network through the eBird portal, Cornell Laboratory of Ornithology, Ithaca, New York, USA. We made extensive use of audio recording for identification and documentation, and our recordings have been archived at the Macaulay Library (ML), Cornell Laboratory of Ornithology, Ithaca, New York, USA. We mist-netted birds in focal habitats at each primary study site and obtained measurements and photographs of many species (Table 1, Appendix). We collected voucher specimens and tissue samples of select species (Appendix), which are deposited at the Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru; the Cornell University Museum of Vertebrates (CUMV), Ithaca, New York; and the Kansas University Natural History Museum (KUNHM), Lawrence, Kansas. Common and scientific names of birds follow Gill and Donsker (2010).

RESULTS

We recorded 462 bird species representing 52 families above 900 m elevation in the study region. About 110 of the 462 species recorded above 900 m represent first records for the Department of Ucayali (T. S. Schulenberg, pers. comm.). Information on distribution among the study sites, relative abundance, habitat, documentation, and conservation status for each species is in the Appendix.

Pajonal Bird Community.—We recorded 106 bird species representing 30 families in the pajonales, and detected 61 species only in this habitat. Tyrannidae (22 species) and Thraupidae (17 species) were the most diverse families. Most species were encountered in the shrub-dominated, marginal, and secondary pajonales than in the grass-dominated pajonales and pastures.

Montane Bird Community.—We detected 300 bird species representing 45 families across all humid montane habitats (i.e., paramo, elfin forest, and upper and lower montane evergreen forest).
Trochilidae (24 species), Furnariidae (26 species), Thamnophilidae (26 species), Tyrannidae (38 species), and Thraupidae (40 species) contributed most to species richness. Habitats at higher elevations were less diverse than those at lower elevations with elfin forest (35 species) and paramo grassland (5 species) having the lowest diversity. The stunted forest on fine white substrate was also depauperate with only Golden-olive Woodpecker (Colaptes rubiginosus), Rufous-vented Tapaculo (Scytalopus femoralis), and occasional canopy flocks.

Status.—We recorded 12 presumed Boreal and 15 presumed Austral migrant bird species during the inventory (Appendix), which straddled the time period of arrival of Boreal migrants and departure of Austral migrants. Two migrant species, Black-and-white Tanager (Conothraupis mexicana) and Black-and-white Seedeater (Sporophila lactuosa), do not fit into either the Boreal or Austral migrant category, and Red-eyed Vireo (Vireo olivaceus) was likely represented by migrants from both the north and south. Additional work in the region at other seasons is needed to confirm the migratory status of some species. Nesting activity in the form of an active nest or dependent young was documented only for Blue-fronted Lancebill (Doryfera johannae), Swallow-winged Puffbird (Chelileia tenebrosa), Golden-olive Woodpecker, Slaty-capped Flycatcher (Leptopogon superciliiaris), Social Flycatcher (Myioborus similis), Great Kiskadee (Pitangus sulphuratus), Spotted Nightingale-Thrush (Catharus dryas), and Wedge-tailed Grass Finch (Emberizoides herbicola). We noted breeding condition (brood patch or cloacal protuberance) among an additional 15 species captured in mist nets (Appendix). Two mist-netted Large Elaenia (Elaenia spectabilis), almost certainly a migrant in the region, and a Mosaic-colored Tyrannulet (Phaeomyias murina) had old brood patches. Representatives of 27 of the 89 species captured in mist nets were actively molting (Appendix).

Species Accounts.—We obtained new data for 22 species previously unknown from the region, of extremely local distribution, or of uncertain taxonomic status.

Brown Tinamou (Crypturellus obsoletus).—This species was detected in forested habitats at seven of eight study sites, including Monte Tabor and the upper Shaani Valley, where it was fairly common to common. Birds from south of the Unine River generally occurred at lower elevations and gave songs and calls (ML 138701, 140407, 140428, 140429) that differed from songs and calls given by birds north of the Unine River (ML 138807, 138862, 140539, 140546, 140582). Additional work on morphological and vocal variation is needed to clarify the taxonomic status of populations here and elsewhere in the range of this widespread species.

Northern/Southern Caraeara (Caracara spp.).—We observed this species near the air strip in Oventeni on 13 September 2008. The caraeara was seen well from below, but the brevity of this observation precluded specific identification. There have been scattered sight records of Southern Caraeara (C. planiceps) in the Peruvian Amazon, the northernmost at the Rio Cushabatay in Loreto (B. P. Walker, unpubl. data), and Yanachaga-Chemillen National Park in Pasco (J. J. Chalco and Thomas Arndt, unpubl. data). This constitutes the first record of the genus Caracara for Ucayali.

Russet-crowned Crake (Laterallus viridis).—This species was fairly common in tall grass savanna at Monte Tabor and in shrub-dominated savanna around Oventeni, where we collected a single male. Individuals were most often detected when a pair uttered a descending duet from dense vegetation, often counter-singing with pairs on adjacent territories. This species is patchily distributed in Peru with the nearest records from the Apurimac and Chanchamayo valleys (Taczanowski 1886, Bond 1955; pers. obs.). These constitute the first records for Ucayali.

Picui Ground-Dove (Columbina picui).—One individual was observed and photographed on 13 September 2008 in dense, recently burned shrub-dominated savanna in Oventeni. This austral migrant is known in Peru largely from the Madre de Dios drainage in the southern Amazon, and the only prior records in Ucayali are from Yarinacocha (Pearson 1975) and Balta (O’Neill 1969).

Spot-tailed Nightjar (Caprimulgus maculicollis).—This species was fairly common in recently burned savanna and pasture at Oventeni. Both photographs and audio recordings were obtained. Patchily distributed in Peru, this species is known from savanna and dry inter-Andean valleys, the nearest records being 400 km to the north in the Mayo Valley (Begazo et al. 2001). These constitute the first records for Ucayali.

New barbet form (Capito taxum novum).—A form of Capito barbet allied to Scarlet-banded
Barbet (Capito wallacei) of the Cordillera Azul in Loreto, Peru was fairly common at the upper Shinipo Valley site and also detected in the upper Tzipani Valley. Four male and four female specimens as well as photographs and recordings were obtained. A more complete description of this taxon will be presented elsewhere.

Cinerceous-breasted Spinetail (Synallaxis hypospodia).—We found this species fairly common both in grassy savanna at Monte Tabor and in shrub-dominated savanna at Oventeni. We obtained one male and one female specimen as well as photographs and audio recordings. S. hypospodia was previously known in Peru from only three isolated localities: the Mayo River drainage (D. F. Lane, unpubl. data), the Urubamba Valley (von Berlepsch and Stolzmann 1906, Chapman 1921), and Pampas del Heath (Louisiana State University Museum of Natural Science [LSUMNS] specimens). Our observations constitute the first records for Ucayali.

Rusty-backed Antwren (Formicivora rufa).—This species was fairly common in shrub-dominated savanna at Oventeni, but also present in taller graminaceous savanna at Monte Tabor. Single male and female specimens were obtained, as were photographs and audio recordings. This species is known in Peru only from three locations: the Huallaga Valley (Bond 1955), Urubamba Valley (von Berlepsch and Stolzmann 1906, Chapman 1921), and Pampas del Heath (LSUMNS specimens). These records are the first for Ucayali.

White-browed Antbird (Myrmoborus leucophrys koenigorum).—This species was uncommon to fairly common in more xeromorphic woodland with dense understory and forest patches bordering savanna at Monte Tabor and Oventeni, where we obtained photographs and audio recordings. Most birds observed appeared to represent the subspecies koenigorum based on their extensive white caps and relatively dark underparts. This recently-described subspecies is known previously only from the Huallaga Valley in Huánuco, San Martín, and adjacent Ucayali (D. F. Lane and B. P. Walker, unpubl. data; LSUMNS specimens). However, as noted for the Huallaga Valley (O’Neill and Parker 1997), we found that some individuals had relatively dark caps resembling the nominate subspecies of the Amazonian lowlands. Further research into the taxonomic status of these populations is needed.

Barred Antthrush (Chamaea malissina).—A single individual of this species was heard on 2 and 4 October 2008 in montane evergreen forest at 1,900 m along the ridge separating the Rio Tzipani and Rio Shaani watersheds. A recording was obtained on 2 October. Short-tailed Antthrush (C. campanisora) was common at lower elevations in transitional forest, but Barred Antthrush was the only Chamaea detected in humid montane forest at high elevation. This locality is within what was thought to be a gap in the distribution of this species, previously known in Peru only from north of the Mayo Valley and southeast of the Apurimac Valley (Schulenberg et al. 2007).

Plain-backed Antpitta (Grallaria haplomela).—Two individuals were recorded in montane evergreen forest at 1,850–1,900 m in the upper Shaani Valley and later identified (D. F. Lane and T. S. Schulenberg, pers. comm.). This is a significant southward extension from the current range limit of this species in San Martín north of the Mayo Valley (Schulenberg et al. 2007).

Tapaculo species (Scytalopus spp.).—We found two taxa of Scytalopus that apparently replace each other elevationally in the southern Sira and Gran Pajonal. Birds with vocalizations consistent with the Peruvian endemic Rufous-vented Tapaculo were regularly heard and recorded, and rarely glimpsed between 1,700 and 2,200 m. The song of this taxon was a single note repeated at 1–4 notes/sec usually for 30 sec or longer. This species was one of the more common birds by voice both in the upper Shaani Valley and in elfin forest, and even patches of scrub up to just below the summit of Menkorenem. A faster-paced Scytalopus song was heard and recorded between 1,400 and 1,600 m in the upper Santeni Valley and at Cerro Quitchungari. This song consisted of a single note repeated at a rate of 7–9 notes/sec, often for 12 to 20 sec. Each phrase was frequently initiated with an excited rising-descending jumble of faster-paced notes. This song type is consistent with the songs of southern populations of Northern White-crowned Tapaculo (Scytalopus atratus) in the Cordillera Azul and Cuzco (Krabe and Schlenberg 1997; D. F. Lane, pers. comm.).

Sooty-headed/Yungas Tyrannulet (Phyllomyias griseiceps/weedeni).—A tyrannulet species was fairly common in forest patches at Oventeni, and also recorded in the upper Santeni Valley, at Monte Tabor, and at Cerro Quitchungari. Photographs and audio recordings were obtained. Songs given by individuals appear to be intermediate between those of these similar species, containing
clear whistled notes reminiscent of Yungas
followed by a chatter resembling that of Sooty-
headed. Further research into morphological and
vocal variation within and between these very
similar taxa is warranted.

Sharpbill (Oxycerus cristatus).—Three sing-
ing birds were in montane evergreen forest at 1,500 m in the Santeni Valley on the western side
of the Sira cordillera. Photographs and audio
recordings were obtained. These three birds sang
in rotation from the tops of particular trees within
200 m of each other, behavior consistent with that
observed at explored leks in Costa Rica (Stiles
and Whitney 1983). One individual was also
heard lower down the same ridge at 1,200 m, also
in the Santeni Valley. We did not detect this
species at suitable elevations on the eastern side
of the cordillera, where we focused much more
effort. This species is spottily distributed on
outlying ridges in Peru (Davis 1986). O. cristatus
had not previously been recorded in the Cerros del
Sira.

Wing-banded Wren (Microcerculus hamhla).—
One individual was observed and recorded at
1,600 m in the upper Shinipo Valley, and two
birds were heard at 1,200 m near Huerto Eden
west of Cerro Quitchungari. Two additional
individuals were recorded at lower elevations
(400-800 m) at Sapan in the Ucayali Valley.
Curiously patchy in distribution, M. hamhla has
been recorded several times in the foothills of
central Peru (Mee et al. 2002, LSUMNS speci-
mens; M. J. Miller, unpubl. data).

Pipit species (Anthus spp.).—One individual
was observed on 2, 5, and 6 October 2008 at
2,200 m elevation just below the summit of
Menkoremon. We generally observed this indi-
cidual in short, grassy paramo, particularly in
wetter areas with muddy substrates. It typically
flushed close underfoot before flying some
distance, often 100 m or more, and dropping
down into a taller patch of grass. We did not hear
this bird call, nor were we able to secure a
specimen or photographs. Our observations indi-
cate the bird was relatively pale with contrasting
white outer tail feathers, but are insufficient for
specific identification.

Sira Tanager (Tangara phillipsii).—This species
was uncommon in the elfin forest near treeline on
Menkoremon, but locally common in montane
evergreen forest in the upper Shaani Valley. We
also recorded one individual in short forest at the
edge of a landslide in the upper Santeni Valley.

We obtained audio recordings and photographs of
both males and females. This species appeared to
favor open habitats or edges over forest interior. It
was most frequently encountered in elfin forest, in
the stunted forest on fine substrates, or along the
openings over streams. We recorded this species
between 1,600 and 2,200 m, higher than the
previous records at between 1,300 and 1,570 m
(Graves and Weske 1987, Mee et al. 2002). This
species frequently occurred in groups of between
two and 15 individuals that associated with
mixed-species feeding flocks in the canopy or
sub-canopy. Other species in these flocks included
Montane (Lepidocolaptes lacrymiger) and Olive-
backed (Xiphorynchus triangularis) woodcreep-
ers; Mottle-checked Tyrannulet (Phylloscartes
ventralis); Blue-winged Mountain-Tanager (Ani-
sognatithus somptuosus); Flame-faced (Tangaro
parzudakii), Beryl-spangled (T. nigroviridis),
Saffron-crowned (T. xanthocephalus), Vermilion
(Calochauetes coccineus), and Yellow-throated
(Iridosornis analis) tanagers; Golden-collared
Honeycreeper (Iridophanes piciterrimus), and
Bluish (Diglossa caerulescens) and Golden-eyed
(D. glauca) flowerpiercers. This species was
previously known only from the northern Cerros
del Sira, 150 km north of our study sites (Graves
and Weske 1987, Mee et al. 2002). Its presence in
the southern Sira suggests a more or less
continuous distribution at higher elevations along
the Sira cordillera.

Wedge-tailed Grass Finch.—This species was
common in grassy savanna at Monte Tabor and in
primarily herbaceous savanna around Oventeni.
We obtained photographs and audio recordings of
individuals at both localities. We also mist-netted
and measured a single juvenile at Monte Tabor.
We located, measured, and photographed a nest
with two eggs that was probably of this species in
short grass at Monte Tabor on 7 September 2008.
This species was previously known in Peru from
only the Marañon and Mayo drainages to the
north (LSUMNS 88734; D. F. Lane, unpubl. data;
Todd Mark, unpubl. data) and the Pampas del
Heath to the southeast (Graham et al. 1980).
These records constitute a range extension of
600 km and the first records for Ucayali.

Grassland Sparrow (Ammodramus humeralis).—This species was common but secretive in
short grassy savanna at Monte Tabor. At least six
individuals were observed at Monte Tabor,
including one juvenile on 7 September 2008.
Four individuals were observed in fields west of
the town of Oventeni, where sympatric with Yellow-browed Sparrow (*A. aurifrons*), one of the most common birds in this area. We obtained photographs and audio recordings of several individuals. Birds sang regularly early and late in the day, at which time they could at times be observed at length as they perched in an exposed location. Widespread in grasslands in more open parts of South America, the nearest known populations of Grassland Sparrow to the Gran Pajonal are at Pampas del Heath and in cleared lands around Puerto Maldonado, 600 km southeast (Graham et al. 1980; B. P. Walker, unpubl. data). Our records constitute the first for Ucayali and the first from isolated patches of savanna in the eastern Andes.

**Plumbeous Seedeater** (*Sporophila plumbea*).—This species was uncommon in short graminaceous savanna at Monte Tabor and fairly common in pasture and recently burned savanna at Oventeni. We obtained two male specimens as well as photographs and audio recordings. The birds were generally observed in small groups containing both male and female-plumage individuals, but occasionally alone or in flocks of up to 10 individuals. They often associated in Oventeni with large groups of primarily Blue-black Grassquit (*Volatinia jocarina*) in grassy or recently burned areas. Plumbeous Seedeater has a similar global distribution to Grassland Sparrow, and in Peru is known only from the Pampas del Heath (Graham et al. 1980). This species may be a non-breeding visitor to the Gran Pajonal from breeding areas further south; neither male collected was in breeding condition (testes ≈ 1 × 1 mm).

**Black-billed Seed Finch** (*Oryzoborus atrirstris*).—A male singing from a marsh of tall reeds bordering dry savanna in Oventeni throughout the day on 19 September 2008 was photographed and recorded. We did not detect this bird despite coverage of this area prior to 19 September, but its near-continuous song and strong response to audio playback appeared to be territorial behavior. It is possible this bird’s arrival was related to the appearance of large roosting aggregations of Black-and-white and Yellow-hellied (*Sporophila nigricollis*) seedeaters in this marsh beginning about 17 September. Rare and patchily distributed in eastern Peru, most records of Black-billed Seed-Finch come from near the base of the Andes. The only previous record from Ucayali was along the Abujae River well to the east (LSUMNS specimens).

**DISCUSSION**

**Biogeography.**—In addition to the 462 bird species we recorded, 57 species are known from above 900 m only in the northern Cerros del Sira (J. S. Weske and J. W. Terborgh, unpubl. data; Mee et al. 2002), bringing the regional species total to 519. These totals are preliminary and there are few equivalent surveys for comparison, but it is clear the Gran Pajonal and southern Cerros del Sira support high levels of avian diversity.

The majority of the birds we found in the *pajonales* are widespread in disturbed areas, anthropogenic or otherwise, in lowland Amazonia or the lower slopes of the Andes. Other species are restricted to regions with better-developed neotropical savannas (e.g., the Venezuelan llanos or Bolivian pampas) but occur patchily in isolated dry valleys of the eastern Andes (Chapman 1921, Robins et al. 1999, Aleixo and Poletto 2007). This list includes Tataupa Tinamou (*Crypturellus tatanqua*), Russet-crowned Crane (*Grus rubicundus*), Black-faced Tanager (*Schiornis flavogaster*), Subtropical Pygmy Owl (*Glaucidium sensitum*), and Wedge-tailed Grass Finch. Plumbeous Seedeater and Grassland Sparrow are unique as they are widespread in neotropical savannas elsewhere, but were not previously known from isolated savannas in the eastern Andes (Graham et al. 1980). It is not obvious whether the above species have maintained relictual populations in this region or whether colonization has occurred more recently. Resolving this question may provide insight into origins of the *pajonales*.

The majority of the avifauna of humid montane habitats represents a subset of that found in these habitats on the eastern slopes of the Andes that are closest to the Cerros del Sira in the departments of Junín, Pasco, and Huánuco (Schulenberg et al. 1984; pers. obs.). Some species detected, however, occur on multiple isolated Andean ridges, but not on the principal cordillera of the Andes. Of these, Subtropical Pygmy Owl (*Glaucidium parkeri*), Koeck’s Hermit (*Phaethornis koeckei*), Rufous-webbed Brilliant (*Heliodoxa bractickii*), Rough-legged Tyrannulet (*Phyllonyx humei*), Sooty-headed/Yungas Tyrannulet, Buff-throated Tody-Tyrant (*Hemitriccus rugularis*), Brazilian Laniomma (*Laniomma elegans*), Sharp-tailed Pipa (*Snowornis subalaris*) were recorded. Two other species of isolated
Andean ridges detected in the northern Sira (J. S. Weske and J. W. Terborgh, unpubl. data), Rufous-brown Solitaire (Cithaerias leucogenys) and Roraiman Flycatcher (Myiophobus roraimae), were not found during our surveys. These "outlying ridge species" are hypothesized to be relicual taxa that became extinct along the main Andean chain but persist due to lack of competition in the relatively depauperate avian communities on outlying ridges (Terborgh and Weske 1975, Fitzpatrick et al. 1977). Further investigation of this peculiar biogeographic pattern is warranted.

CONSERVATION IMPLICATIONS

The new barbet form and Sira Tanager are of particular conservation concern because their global distributions are restricted to the Sira. Large cracids such as Wattled Guan (Atrura atra) and Spix's Guan (Penelope jacuquestra), appear to maintain healthy populations in the southern Cerros del Sira and Gran Pajonal, but deserve special consideration because they are threatened by hunting in many areas (Strahl et al. 1994). The endemic koeckae subspecies of Horned Curassow (Pauxi unicornis) was not detected during our inventory, but it may well be present at low densities and merits urgent conservation action because of its small range and apparent susceptibility to hunting pressure (Gustadaga et al. 2007, Graham 2009).

Both lower montane forest and savanna are habitats of conservation priority in South America (Silva 1995, Stotz et al. 1996, Renjifo et al. 1997). The patches of these habitats within the study region deserve special attention because of their isolation and unique avian communities. The montane evergreen forests of the Sira have received some protection since a portion of the range was designated a communal reserve in 2001 (Benavides 2005). The pajonales of the Gran Pajonal receive no official protection and are particularly susceptible to changes in land use by humans. Conservation of bird habitat in the Gran Pajonal by outside interests would be a complex task; the pajonales are maintained by the Asheninka for spiritual and agricultural reasons (Hvalkof 2006), but exist in a mosaic of disturbed habitats impacted by both traditional Asheninka practices as well as land use by colonists. Our fieldwork indicates the region supports several bird species of open habitats that are rare or range-restricted in Peru. There are currently few protected areas of savanna or seasonally dry forest in inter-Andean valleys of Peru where these species are found (Linares-Palomino 2006, Angulo et al. 2008). Any conservation strategy will depend on the support of the local Asheninka and should incorporate their interests.

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LITERATURE CITED


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### APPENDIX. Status of birds above 900 m elevation in the Gran Pajonal and southern Cerros del Sira, Perú, 2008.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Monte Tabor</th>
<th>Overen-demen</th>
<th>Menkonen Valley</th>
<th>Shami Valley</th>
<th>Stimpe Valley</th>
<th>Santeini Valley</th>
<th>Tzapuni Valley</th>
<th>Quechumungari</th>
<th>Northern Sites</th>
<th>Elevation (m)</th>
<th>Habitat</th>
<th>Status</th>
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Notes:
- **A** indicates a species that was observed to be abundant at the site.
- **P** indicates a species that was observed to be present at the site.
- **S_p** indicates a species that was observed to be present at the site but not abundant.
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\(^1\) Northern Site: Location where the species was observed.
\(^2\) Elevation (m): Elevation range in meters.
\(^3\) Habitat and Status: Habitat preferences and status classification.
### APPENDIX. Continued.

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### APPENDIX. Continued.

| Scientific name                     | Monte Taber | Oren-teen | Menikoreen | Shuani Valley | Shuipo Valley | Sansen Valley | Tripani Valley | Quichangari | Northern Site | Elevation (m) | Habitat $^1$ | Status $^2$ | Documentation $^3$ |
|-------------------------------------|-------------|-----------|------------|---------------|---------------|---------------|----------------|--------------|---------------|---------------|--------------|------------|------------|----------------|
| **Ochthoea pulchella**              | U           | X         |            |               |               |               |                |              | X             | -             | -           | -          | -           |
| *Colonia colonus*                   | F           | C         | R          | X             | X             |               |                |              | L-1,550       | S_p          | A          | -          | -           |
| *Legatus leucocephalus*             | F           |           |            |               |               |               |                |              | L-1,400       | S_p          | -          | -          | -           |
| *Myiobates simillis*                | F           |           |            |               |               |               | X              |              | L-1,050       | S_p          | -          | -          | -           |
| *Pluagus sulphuratus*               | F           |           |            |               |               |               | X              |              | L-1,050       | F_p, S_p     | r          | A          | -           |
| *Philohydror lictor*                | R           |           |            |               |               |               |                |              | 1,050         | R            |            |            | -           |
| *Conophas cinchonell*               | R           |           |            |               |               |               |                |              | 1,100         | F_i          | A          | -          | -           |
| **Myiodynastes chrysocephalus**     | R           |           |            |               |               |               |                |              | L-1,050       | F_i          | a          |            | -           |
| *M. maculatus*                      | F           | C         | X          | X             | X             | X             | X              | X            | L-1,500       | F_i, S_p, F_t | a$^*$?    | A          | -           |
| *Empidonomus varius*                | R           |           |            |               |               |               |                |              | L-1,050       | F_i          | -          | a          | -           |
| *Grisoetonymus aurantiacrotcrisatus*| R           |           |            |               |               |               |                |              | -             | -            | A          |            | -           |
| *Tyranus melanochilus*              | C           | C         | X          | X             | X             | X             | X              | X            | L-1,550       | S_p          | -          | -          | -           |
| *Rhytipherna simplex*               | F           |           | F          | X             | X             | X             |                | X            | L-1,400       | F_p, F_t     | A          | -          | -           |
| *Myiarchus tuberculifer*            | R           | U         | X          | X             |               |               |                |              | L-1,000       | F_i          | A          | -          | -           |
| *M. cephalotes*                     | R           |           |            | X             |               |               |                | X            | X-1,400-1,900 | F_m, F_m     | A          | A          | -           |
| *Attila spodiceus*                  | R           |           | C          | X             | X             |               |                | X            | 1,850         | F_m          | A          | -          | -           |
| *Amphion rufifassila*                | F           |           |            |               |               |               |                | X            | -             | -            | A          | -          | -           |
| *Pipreola riefferi*                 | C           | U         | X          | X             |               |               |                | X            | 1,800-2,000   | F_m          | -          | r, p        | M, P, A     |
| *P. pulchra*                        |              |           |            |               |               |               |                |              | 900-1,100     | F_i          | A          |            | -           |
| **P. frontalis**                    |             |           |            |               |               |               |                |              | 1,000-1,250   | F_t          | n          | A          | -           |
| *P. chloronellida*                  |              |           |            |               |               |               |                |              | 900-1,500     | F_t          | A          |            | -           |
| *Ampelioideis tschudii*             | U           |           | F          | X             | X             | X             | X              | X            | 900-1,800     | F_m, F_m     | P          | -          | -           |
| *Rupicola peruvianus*                | U           |           | U          |               |               |               | X              |               | L-1,000       | F_i          | A          | -          | -           |
| *Lipagus vociferans*                | U           |           | R          | X             | X             | X             | X              | X            | 1,100-1,400   | F_i          | S_2        | -          | -           |
| *Snowornis subalaris*               |              |           |            |               |               |               |                |              | 1,850-1,900   | F_m          | A          | -          | -           |
| *S. cryptopus*                      |              |           |            |               |               |               |                |              | L-1,100       | F_i          | A          | -          | -           |
| *Querula purpureata*                | U           |           | C          |               |               |               |                | X            | L-1,050       | F_i, S_p     | M, P, A     | -          | -           |
| *Machaeoripinnia pyrocepehalis*      |              |           |            |               |               |               |                |              | 900-1,350     | F_t          | P          | A          | -           |
| *Lepidothris coronata*               |              |           |            |               |               |               |                | X            | 1,250         | F_t          | -          | -          | -           |
| *L. coeruleocephala*                |              |           |            |               |               |               |                | F            | 1,000-1,350   | F_t          | P          | A          | -           |
| *Xenopipra holochilota*              | U           | R         | X          | X             |               |               |                | X            | 1,000-1,850   | F_m, F_m     | M, P        | -           | -           |

$^1$ Habitat: A = alder, P = pine, S = spruce

$^2$ Status: A = new, O = newly observed, M = new

$^3$ Documentation: M = new, P = newly observed, A = new

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* C = common (more than 10 individuals per observer per day); F = fairly common (1-10 individuals per observer per day); U = uncommon (recorded less than daily but on at least 25% of days per observer); R = rare (recorded on less than 25% of days per observer); X = present (coverage at site insufficient to estimate abundance).
* This column includes species recorded above 900 m in the northern Cerros del Sira (S. J. Socorro, J. S. Wesley, and J. W. Terborgh, unpubl. data; Mee et al. 2001).
* L = Lowlands.
* P = Pampa; F_m = forest; F_p = upper montane evergreen forest; F_t = lower montane evergreen forest; F_l = tropical lowland evergreen forest; S_p = pajonal; M = marsh; R = rivers and streams.
* b = boreal migrant; a = Austral migrant; n = other migration strategy; * = in part (resident individuals also occur); c = reproductive activity noted; m = active molt noted; e = endangered; v = vulnerable; n = near-threatened; p = Pernesian endemic (Stots et al. 1996, IUCN 2009).
* S = specimen collected by author; S_p = specimen collected by Andrews Museum (deposited in the American Museum of Natural History, New York, USA); P = photograph in the field or hand; A = audio recordings (deposited in MLA); M = measurements of mist-netted bird.
* T = specimen collected at the Gran Pajonal (Thurleus 1974).
GENETIC BARCODE RFLP ANALYSIS OF THE NELSON’S AND SALTMARSH SPARROW HYBRID ZONE

JENNIFER WALSH, ADRIENNE I. KOVACH, Oksana P. LANE, KATHLEEN M. O’BRIEN, AND KIMBERLY J. BABBITT

ABSTRACT.—Hybridization between Saltmarsh Sparrow (Ammodramus caudacutus) and Nelson’s Sparrow (A. nelsoni) has been documented in areas where the two species occur sympatrically, increasing the difficulty of accurate species identification. We developed a DNA barcoding restriction fragment length polymorphism (RFLP) test to discriminate between Nelson’s Sparrows and Saltmarsh Sparrows and applied it to 426 putative Saltmarsh Sparrow samples from Maine to New York, USA. All individuals were identified in the field as Saltmarsh Sparrows based on morphology, but 34 (8%) had Nelson’s specific mitochondrial DNA, indicating they were of hybrid origin. This discrepancy in morphological and genetic data highlights the difficulties associated with accurate field identification and may hinder conservation efforts by confounding attempts to identify and monitor “pure” populations. Mitochondrial DNA of Nelson’s Sparrow was prevalent at the most southern point of the previously documented overlap zone and was also found in one individual 150 km south of the overlap zone. Our findings offer new insights into the extent of hybridization between the two species and underscore the need for further investigation into the consequences of hybridization on conservation of Saltmarsh Sparrows.

The distribution and taxonomic classification of Nelson’s Sparrow (Ammodramus nelsoni) and Saltmarsh Sparrow (A. caudacutus) have been a topic of ornithological debate for over a century (Greenlaw 1993, Rising and Avise 1993, Shriver et al. 2005). In 1995, the five previously recognized subspecies of A. caudacutus (American Ornithologists’ Union 1957) were split into the two species recognized today. The elevation to species status was based on observed variation in morphological features, mitochondrial DNA (mtDNA), and behavior in Nelson’s and Saltmarsh sparrows (Greenlaw 1993, Rising and Avise 1993) and the assumption of limited interbreeding (American Ornithologists’ Union 1995), despite recommendations for retaining the subspecies classification (Rising and Avise 1993). Both species breed in coastal marshes along the northeastern United States. A subspecies of Nelson’s Sparrow (A. n. subvirgatus) breeds in marshes from coastal Québec to northeastern Massachusetts, and the two subspecies of Saltmarsh Sparrow (A. c. caudacutus and A. c. diversus) breed from Maine to New Jersey and New Jersey to Virginia, respectively (Greenlaw and Wooffenden 2007). The two species occur sympatrically in tidal marshes along the Atlantic Coast, but Nelson’s Sparrows also inhabit less tidal, brackish marshes as well as upland habitats, including grasslands and hayfields (Nocera et al. 2007); Saltmarsh Sparrows are restricted to expansive, intertidal areas that are influenced strongly by tidal flow (Greenlaw 1993, Shriver et al. 2005).

Hybridization between Nelson’s and Saltmarsh sparrows, despite interspecific variation (morphological, behavioral and genetic), has been previously documented within an overlap zone from the Weskeag River estuary in South Thomaston, Knox County, Maine (44° 04.60’ N, 69° 08.66’ W) to Parker River National Wildlife Refuge (NWR) in Newburyport, Essex County, Massachusetts (42° 77.42’ N, 70° 80.86’ W) (Rising and Avise 1993, Hodgman et al. 2002, Shriver et al. 2005). Shriver et al. (2005) found a concordance between genotypic and phenotypic variation in hybrid sparrows from three marshes in southern Maine. The authors suggested hybrids occur wherever the two species are sympatric, which would manifest in a 190-km reduction in the range of “pure” Saltmarsh Sparrow populations. The implications of this range reduction suggest the need for additional research to monitor the rate of occurrence of hybrids in marshes throughout the overlap zone.

Hybridization is common in nature and especially in birds, for which it has been recorded in almost one of 10 species (Grant and Grant 1992). It typically occurs in young pairs of sibling...
species that diverged <1–2 million years ago and, therefore, have not yet evolved reproductive
barriers or hybrid inviability (Mallet 2005). The occurrence of hybridization has been
correlated with many ecological factors including
parasitism, scarcity, and low male parental care
(Neergard 2006). Hybridization and introgression
an lead to harmful effects including hybrid
swamps, outbreeding depression, and reduced
fitness, and can be especially problematic when
one species is less abundant than the other
(Rhymer and Simberloff 1996, Allendorf et al.
2001). Hybridization with an invading conspecific
has been responsible, at least in part, for the
extinction of several threatened species (Rhymer
and Simberloff 1996, Allendorf et al., 2001, Buggs
2001). Thus, it is important to monitor and
consider the impacts of hybridization in Nelson’s
and Saltmarsh sparrows in light of these poten-
tially negative consequences. Both species are a
high conservation priority in the northeastern
United States (USDI 2008), and the Saltmarsh
Sparrow is considered globally vulnerable to
extinction (IUCN Red List criteria; Birdlife
International 2004). This concern is based on the
Saltmarsh Sparrow’s limited range and its oblig-
ate dependence on a narrow strip of heavily-
fragmented coastal marsh habitat that is vulner-
able to anthropogenic degradation and sea level
rise (Gjerdrum et al., 2005, Greenberg et al. 2006).

Expansion of the overlap zone and the potential
for increased hybridization, therefore, may pres-
ent a greater threat to the long-term persistence of
the Saltmarsh Sparrow.

Our objectives were to: (1) develop a diagnostic
assay based on the DNA barcoding region to
identify Saltmarsh Sparrows of hybrid origin, and
(2) evaluate the extent of introgression
throughout the overlap zone.

METHODS

Study Area and Sample Collection.—We used
two to six 12-m mist nets with size 36 mm mesh
to capture adult sparrows. Blood samples (30–
50 µl) were drawn from the cutaneous ulnar vein
using a non-heparinized capillary tube. We
collected one or two tail feathers instead of blood
for a few individuals. Individuals were identified
in the field as either Nelson’s or Saltmarsh
Sparrows by plumage characteristics and mor-
phological measurements (Shriver et al. 2005). We
released all birds within 10–20 min of capture.

Blood samples were stored on Whatman filter
papers at room temperature for later genetic
analysis. All individuals were sampled during
the breeding season (Jun–Aug) and only breeding
adults were used in the analyses (confirmed by the
presence of a brood patch/cloacal protrusion).

We obtained blood or feather samples from
known individuals from outside of the overlap
zone (n = 8 Nelson’s Sparrows from Penobscot
River, Maine; 44° 36.58’ N, 68° 50.58’ W and
n = 8 Saltmarsh Sparrows from Shirley and
Oceanside, New York; 40° 47.50’ N, 72° 53.06’
W and 40° 37.27’ N, 73° 37.38’ W) to develop a
 genetic assay for species identification. Individu-
als were also sampled within the overlap zone, for
which species identification was based on mor-
phological features (O. P. Lane, pers. obs.; n = 4
Saltmarsh Sparrows and n = 3 Nelson’s Sparrows
from Wells and Scarborough, Maine; 43° 16.96’ N,
70° 34.97’ W and 43° 33.90’ N, 70° 21.71’ W). We
obtained field measurements of culmen length
(mm), bill width (mm), and depth (mm) using
digital calipers, and mass (to the nearest 0.1 g) using
digital scales for allopatric Nelson’s and Saltmarsh
Sparrows (n = 34 Nelson’s Sparrows from
Penobscot River, Maine and n = 29 Saltmarsh
Sparrows from Shirley, New York). One individual
made all bill measurements and weights, and
performed all species identifications in the field.

We applied our genetic test to 426 samples
collected from putative Saltmarsh Sparrows
during ongoing toxicological (Lane and Evers
2007, Lane et al., 2008) and population genetics
(Walsh 2009) research. Our purpose was to
identify sparrows of hybrid origin by a mismatch
between morphology and mtDNA. We focused on
introgression of Nelson’s mtDNA into Saltmarsh
Sparrows, as our samples were collected only
from individuals identified morphologically as
Saltmarsh Sparrow. Samples were collected from
nine marshes along the northeastern U.S. from
2006 to 2008 (Fig. 1). Study marshes were in
Wells, Maine (Rachel Carson NWR; 43° 16.96’
N, 70° 34.97’ W; Scarborough, Maine (Scarbor-
ough State Wildlife Management Area; 43° 33.90’
N, 70° 21.71’ W); Hampton, New Hampshire (42°
55.66’ N, 70° 48.65’ W); Rye, New Hampshire
(43° 20.24’ N, 70° 43.27’ W); Stratham, New
Hampshire (43° 20.44’ N, 70° 55.48’ W); New-
buryport, Massachusetts (Parker River NWR; 42°
46.45’ N, 70° 48.51’ W); Narragansett, Rhode
Island (John H. Chafee NWR; 41° 27.41’ N, 71°
26.88’ W); Shirley, New York (Wertheim NWR;
40° 47.50’ N, 72° 53.06’ W); and Oceanside, New
Genetic Identification.—We used a DNA barcoding approach (Hebert et al. 2003) to develop our assay for species identification. DNA was extracted from known Nelson’s (11) and Saltmarsh sparrow (12) samples using a DNeasy Blood Kit (Qiagen, Valencia, CA, USA). Universal avian primers (BirdF1 and BirdR2) were used to amplify a 648 base pair region of the cytochrome c oxidase 1 (COI) gene in a 12.5 µl polymerase chain reaction following Hebert et al. (2004). Samples were sequenced by Geneway Research LLC (Hayward, CA, USA) or by the Hubbard Center for Genome Studies at the University of New Hampshire.

Nelson’s and Saltmarsh sparrow sequences (GenBank accession numbers HM230725-HM230747) were edited and aligned in Geneious Pro 4.7.6 (Biomatters Ltd, Auckland, NZ) to identify variation within and between species. We included three Nelson’s Sparrow sequences from GenBank (accession numbers DQ433298, DQ432709, and DQ432708) in our alignment. These specimens originated from Minnesota and Illinois (midwestern U.S.) and were identical to the sequences from our Nelson’s reference individuals despite being representative of a different subspecies (A. n. nelsoni).

We found seven diagnostic nucleotide differences between Nelson’s and Saltmarsh sparrows. We identified a single nucleotide difference in a
TABLE 1. Mean and standard errors for four morphological features compared across three groups (Nelson’s Sparrow, Saltmarsh Sparrow, and hybrids). Values with different letters are significantly different based on a Tukey’s test.

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<td>8.42 ± 0.06 (B)</td>
<td>9.22 ± 0.08 (A)</td>
<td>9.26 ± 0.09 (A)</td>
</tr>
<tr>
<td>Bill width, mm</td>
<td>4.02 ± 0.04 (B)</td>
<td>4.42 ± 0.05 (A)</td>
<td>4.31 ± 0.05 (A)</td>
</tr>
<tr>
<td>Bill depth, mm</td>
<td>5.01 ± 0.03 (B)</td>
<td>5.12 ± 0.04 (A)</td>
<td>5.26 ± 0.04 (A)</td>
</tr>
<tr>
<td>Body mass, g</td>
<td>17.32 ± 0.25 (B)</td>
<td>18.57 ± 0.28 (A)</td>
<td>18.96 ± 0.27 (A)</td>
</tr>
</tbody>
</table>

Hinf specific restriction site and used it as the basis for the development of a species-specific diagnostic assay. Amplified products were digested in a 10.5 µl reaction (9 µl template DNA, 0.5 µl enzyme HinfI, and 1.0 µl of NEBuffer 4: New England BioLabs, Ipswich, MA, USA) and incubated overnight at 37 °C. This restriction fragment length polymorphism (RFLP) analysis yielded two fragments (~100 and 550 base pairs in size) in Saltmarsh Sparrows, and three fragments (~100, 150, and 400 base pairs in size) in Nelson’s Sparrows when resolved on a 3% agarose gel.

We applied the diagnostic assay to the 426 individuals identified morphologically (based on plumage and morphometrics) as Saltmarsh Sparrows from Maine to New York. Individuals with Nelson’s mtDNA were considered putative hybrids. These individuals were sequenced to confirm consistency among introgressed individuals.

Morphological Comparisons.—We compared morphometric data of the putative hybrids (identified by our genetic assay as having Nelson’s mtDNA) to those of the allopatric Nelson’s and Saltmarsh sparrows sampled outside of the overlap zone (from the Penobscot River in Maine, and Shirley and Oceanside, New York). Averages and standard errors were calculated for the four morphological features for the three groups (hybrid, n = 33; Nelson’s, n = 34; and Saltmarsh, n = 39). ANOVA and a Tukey’s test were used to assess differences in morphological characteristics among the three groups and significance testing was performed using a Bonferroni correction in Program JMP 8 (SAS Institute 2008).

RESULTS

We consistently found the same species-specific nucleotide variations at seven sites (1.2% interspecific variation) when comparing Nelson’s and Saltmarsh sparrow sequences at the COI region. Sequences showed no signs of double peaks, confirming that only mtDNA was amplified. The absence of additional fragments or chimeric samples in the RFLP test also indicated nuclear copies of mtDNA were not amplified. There was no intraspecific variation within these seven sites with the exception of one Saltmarsh Sparrow at one nucleotide site (which was not within the restriction site), nor when comparing our Nelson’s samples with those on GenBank.

Results from our genetic assay revealed that 34 of 426 (8%) putative Saltmarsh Sparrows had Nelson’s mtDNA (Fig. 1: pie charts). Over half (18) of the sparrows with Nelson’s mtDNA were captured in Parker River NWR, Newburyport, Massachusetts (Fig. 1: pie charts). The most southern site at which we identified an individual with Nelson’s mtDNA was in John H. Chafee NWR in Narragansett, Rhode Island (1 of 54 individuals). Sequences from the 34 individuals identified as putative hybrids were all consistent with sequences from Nelson’s Sparrows at the seven diagnostic nucleotide sites.

Results from the ANOVA indicated significant differences in mass ($F_{2.775} = 10.5, P < 0.0001$), bill depth ($F_{2.75} = 10.5, P < 0.0001$), bill width ($F_{2.75} = 20.9, P < 0.0001$), and culmen length ($F_{2.75} = 40.1, P < 0.0001$). Tukey’s pairwise comparisons of the four morphological variables indicated bill measurements and body mass were significantly smaller in pure Nelson’s Sparrow individuals than pure Saltmarsh Sparrow individuals. Hybrid measurements were statistically indistinguishable from those of Saltmarsh Sparrows and larger then those of Nelson’s Sparrows (Table 1).
Interspecific variation between Saltmarsh and Nelson’s sparrows was low, but consistent with seven diagnostic nucleotide differences and a 1.2% sequence divergence at the COI gene. The DNA barcode RFLP approach developed in this study, given the order of magnitude smaller intraspecific variation (0-0.2%), is appropriate for differentiating the two species. Similar levels of interspecific differentiation were found for these two species in previous studies using mtDNA markers (Rising and Avise 1993, Klicka and Spellman 2007). The low interspecific difference between Saltmarsh and Nelson’s sparrows likely reflects their recent divergence (Rising and Avise 1993) and is comparable to the differentiation of other young and hybridizing avian sibling species pairs (Kerr et al. 2007).

We found Nelson’s specific mtDNA in 8% of individuals identified morphologically as Saltmarsh Sparrows, indicating they were of hybrid origin or genetically introgressed. We found evidence of introgression in all but one of six marshes (Rye, New Hampshire) within the overlap zone at a frequency of 3-19%. The relatively high proportion of introgressed individuals in the southern portion of the overlap zone (e.g., 14% at Chapman’s Landing, New Hampshire and 19% at Parker River NWR, Massachusetts) indicated genetic introgression may exceed morphological variation (Rhymer and Simberloff 1996, Sattler and Braun 2000, Bronson et al. 2003). Introgressed individuals were morphologically more similar to pure Saltmarsh Sparrows than to Nelson’s Sparrows, consistent with the findings of Shriver et al. (2005). The lack of a clear “intermediate” hybrid phenotype in the individuals we identified with Nelson’s mtDNA suggests successful backcrossing, which appears to be asymmetrical and biased toward Saltmarsh Sparrows. Shriver et al. (2005) reported similar patterns of microsatellite DNA introgression. Our finding of an introgressed individual at John H. Chafee NWR, Rhode Island raises concern for the potential expansion of the hybrid zone, as this marsh is 150 km south of the southernmost point of the currently assumed hybrid zone (Parker River NWR, Massachusetts).

The morphological similarities between hybrids and Saltmarsh Sparrows may have led to past underestimation of the extent of introgression between Nelson’s and Saltmarsh sparrows and underscores the difficulties of characterizing hybrid zone dynamics. Hodgman et al. (2002), in an extensive survey of New England marshes, monitored 40 points at Parker River NWR and documented a maximum of one Nelson’s Sparrow at 3% of their points in comparison to a maximum of 10 Saltmarsh Sparrows at 78% of their points. Their findings extended the southern range of Nelson’s Sparrow and identified Parker River NWR as the most southern point of the overlap zone. Eighteen (19%) of the 95 putative Saltmarsh Sparrows sampled from Parker River NWR in our study were identified as introgressed (having Nelson’s mtDNA). Our findings suggest a higher incidence of hybridization and, therefore, likely a higher proportion of Nelson’s individuals at Parker River NWR than previously recorded. Previous research on Nelson’s-Saltmarsh hybridization focused on a narrow portion of the overlap zone between the Weskeag River and Webhannet, Maine (Shriver et al. 2005). The discovery by Rising and Avise (1993) of an individual with discordant morphology and mtDNA at Parker River NWR led the authors to conclude the need for further information on interfertilizing between the two species. Shriver et al. (2005) suggested hybrids are present wherever Nelson’s and Saltmarsh sparrows occur sympatrically; the genetic data were not available to support their hypothesis, as they did not sample marshes south of Webhannet, Maine. Our results confirm that introgression is occurring throughout the overlap zone of Nelson’s and Saltmarsh sparrows and there may be a southern expansion of Nelson’s alleles.

The high proportion of introgressed sparrows at Parker River NWR and the potential for an expansion of the hybrid zone have increased significance when the results are compared with a recent population genetic study (Walsh 2009). Microsatellite analyses indicated the sparrows at Parker River NWR are highly connected, by dispersal, to sparrows from other marshes along the northeastern coast. This may have implications for the spread of hybrids, given the large size of this marsh and the potential for large numbers of dispersers originating from Parker River NWR. Emigration from Parker River NWR may result in the spread of Nelson’s alleles further south, and may impact pure Saltmarsh Sparrow populations originally believed to be outside of the overlap zone. Dispersal patterns of hybrids and parental populations largely influence the spatial and
temporal dynamics of hybrid zones. High dispersal rates can lead to maintenance or expansion of a hybrid zone even with selection against hybrids, and introgression can spread to allopatric populations via hybrid dispersal (Barton and Hewitt 1995, Rowher et al. 2001).

The potential for hybrid expansion warrants further consideration of the conservation of genetically pure populations, as hybridization can lead to reduced fitness of parental species through outbreeding depression and loss of local adaptations, as well as the replacement of pure species by hybrid swarms (Rhymer and Simberloff 1996, Allendorf et al. 2001). These consequences are exacerbated when the hybrid zone is moving (Buggs 2007), a situation where Saltmarsh Sparrows are vulnerable due to their small population sizes, potential for asymmetrical outcrossing, human modifications of their habitat, and climate change. Additional research into the behavioral characteristics and fitness of hybrids is needed to evaluate the potential threat of hybridization as one of many stressors currently impacting this threatened species.

Our study was focused only on detecting unidirectional transfer of Nelson’s mtDNA into Saltmarsh Sparrows and did not address the potential for introgression of Saltmarsh Sparrow alleles into Nelson’s Sparrow populations. Our exclusive use of mtDNA enabled us only to detect hybrids with maternal Nelson’s ancestry, possibly leading to an underestimation of the extent of hybridization in Saltmarsh Sparrows. Our data were collected during targeted Saltmarsh Sparrow territories (Lane and Evers 2007, Lane et al. 2008) and population genetics (Walsh 2009) research and not as a study designed specifically to investigate the question of hybridization. Our findings are consistent with patterns of previous studies using both mtDNA (Rising and Avise 1985) and nuclear markers (Shriver et al. 2005), and provide important new insight into the incidence of introgression and the potential expansion of this hybrid zone.

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LITERATURE CITED


THE WHITE-COLLARED KITE (LEPTODON FORBESI SWANN, 1922) AND A REVIEW OF THE TAXONOMY OF THE GREY-HEADED KITE (LEPTODON CAYANENSIS LATHAM, 1790)

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ABSTRACT.—The White-collared Kite (Leptodon forbesi Swann, 1922), previously known by the holotype and three specimens from northeastern Brazil from the late 1880s, is considered by many as a juvenile variant of the Grey-headed Kite (L. cayanensis Latham, 1790). We present new morphological evidence from museum specimens of both species, with a previously misidentified specimen of L. forbesi, and field study to support the validity of the White-collared Kite as a species, now seen as endemic and severely threatened in northeastern Brazil. This species occurs only in remnants of the Atlantic Forest in the states of Alagoas and Pernambuco. It is distinguished from its congener by its white hind-collar, underwing coverts, and leading edge of the wings. The under surface of the secondaries show reduced black barring. The number of white and black tail bands is variable, and not a good diagnostic character. We also review all taxa described for Leptodon and show the described subspecies are not valid. Received 13 May 2010. Accepted 5 November 2010.

There is disagreement about the division of species and subspecies within the genus Leptodon Sundevall, 1836. Some consider this genus to be monotypic and represented only by the Grey-headed Kite (Leptodon cayanensis) (Grossman and Hamlet 1964, Brown and Amadon 1968, Blake 1977, Sick 1997); others consider the White-collared Kite (L. forbesi) a valid species restricted to the Atlantic Forest of northeastern Brazil (Swann 1922, 1945; Teixeira et al. 1987a, Thiolay 1994; Ferguson-Lees and Christie 2001). This latter taxon was described by Swann (1922) as a species based on a single specimen (at the Natural History Museum in Tring, United Kingdom) collected by W. A. Forbes in 1882 in the northeastern Brazilian State of Pernambuco. The White-collared Kite is known from the holotype and three other specimens (at the Museu Nacional do Rio de Janeiro; Teixeira et al. 1987a) with no previous reliable observations (Rodan and Carlos 2003, Silveira et al. 2003, Pereira et al. 2006).

The taxonomic status of the White-collared Kite (Leptodon forbesi), often considered a synonym of L. cayanensis, has been uncertain since the time of its description. Brown and Amadon (1968) consider the holotype specimen of L. forbesi, described by Swann (1922, 1945), as a juvenile plumage variant of the more common and widespread Grey-headed Kite (L. cayanensis). Sick (1997) mentions the high variability of the plumage in L. cayanensis, acknowledged by Foster (1971), as an argument for a similar classification. Hellmayr and Conover (1949) reported the type specimen is a bird in very fresh plumage just finishing its molt, and that presence of an old primary on both wings and some dusky brown feathers on the rump suggest its immaturity. They conclude (1949:26) "while the specimen looks rather different from the ordinary run of L. cayanensis, further material is needed to establish the taxonomic status of L. forbesi beyond doubt". Ferguson-Lees and Christie (2001) concur with Hellmayr and Conover (1949) regarding the morphological description of Leptodon forbesi. They indicate, however, that to consider the type specimen as a juvenile would be a mistake because it has apparently molted recently and has adult plumage with the exception of two or three secondaries and some worn coverts. The traditional diagnosis of Leptodon forbesi include the white underwing coverts; the gray crown; a white collar; white tips on the scapulars, mantle, and wing quills; and a broad white tail band, measuring 60–70 mm (Swann 1945, Hellmayr and Conover 1949, Pinto and Camargo 1961).

The three specimens collected in the 1980s in the State of Alagoas share some similarities with the L. forbesi type specimen. Preliminary analysis
by Teixeira et al. (1987a, b) suggested this taxon differs from L. cayanensis, influencing most of the subsequent literature to treat L. forbesi as a valid species (Forrester 1993, Thiollay 1994. Stotz et al. 1996, Ferguson-Lees and Christie 2001). More recently, Roda and Carlos (2003) found only the Grey-headed Kite in six locations in the states of Alagoas and Pernambuco, but the authors did not present the diagnosis for this taxon. Vocalizations typical of the Grey-headed Kite were also recorded in Alagoas (Silveira et al. 2003), while White-collared Kites were found in southern Pernambuco (Pereira et al. 2006).

The three subspecies of L. cayanensis were based on color differences. Swann (1922) suggests that L. c. cayanensis Latham, 1790 in northern South America (and the Amazon Basin) differs from L. c. monachus Vieillot, 1817 for central and southeastern South America in the following characters: darker black dorsum; dark gray head and nape; upper tail coverts without visible bands, but with some small white spots; black underwing coverts (black and white in L. c. monachus), but with white wing borders (Swann 1922). He further described a third subspecies L. c. mexicanus for Mexico south to Panama, diagnosed by the grayish nape and head; grayish black dorsum; black underwing coverts; upper tail coverts with a whitish-gray band, and grayish black spotted legs.

Hellmayr and Conover (1949) invalidated the subspecies L. c. monachus and L. c. mexicanus because they found no color differences. L. c. mexicanus has since been disregarded in most of the subsequent literature. They indicated that L. cayanensis from Argentina, Brazil, and Bolivia tend to be larger than those in the rest of the range, but offer no analysis to support these conclusions. They also affirm that if the southern form is considered a subspecies, it should be L. c. monachus Vieillot, 1817. This treatment is followed by Thiollay (1994) who lists L. c. cayanensis in the north and L. c. monachus in the south.

The status of the White-collared Kite is classified as ‘Data Deficient’ in the 2003 list of Brazilian animals threatened with extinction as the paucity of museum specimens of L. forbesi has severely hindered the study of its variability. This taxon, if valid, would be critically endangered upon its naming, and it would be among the five most threatened raptors of the world (Thiollay 1994, BirdLife International 2000, Ferguson-Lees and Christie 2001).

We examined differences in morphology between White-collared and Grey-headed kites, and strongly suggest the White-collared Kite is a valid species. We also present arguments in favor of considering the Grey-headed Kite monotypic.

METHODS

We examined 128 specimens within the genus Leptodon (Appendix) from the ornithological collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Nacional do Rio de Janeiro (MN), Natural History Museum at Tring, United Kingdom (NHM), Museum für Naturkunde of the Humboldt-Universität in Berlin (ZMB), Colección Ornitológica Phelps (COP), Instituto de Ciencias Naturales (ICN), and Museo de la Estación Biológica de Rancho Grande (MEBRG). We were unable to obtain permission to examine the Leptodon specimens reported in Teixeira et al. (1987a, b) and they are not included. Additionally, LFS and SS inspected the ornithological collections of the American Museum of Natural History, Natural History Museum Vienna, and National Museum of Natural History (Leiden) in search of specimens pertinent to the taxonomic analysis of L. forbesi-like specimens or from northeastern Brazil), which were not found; thus, these collections are not listed in this paper. The a priori naming of specimens within the genus Leptodon was based on the suggested ranges of the taxa.

We surveyed raptors in forest fragments in the states of Alagoas (AL) and Pernambuco (PE) in October 2007 and February and November 2008. We gathered additional information on morphology, behavior, and abundance of Leptodon (Seipke et al. 2011). Photographs taken in the field were used to supplement the few museum specimens. Vocalizations were opportunistically recorded using a video camera, and used for simple comparison with known recordings of Grey-headed Kites. The areas surveyed were Murici, AL; Usina Serra Grande, São José da Laje, AL; Mata do Córrego, Ibitaguara, AL; Fazenda Varrela, São Miguel dos Campos, AL; Usina Trapiache, Sirinhaem, PE; and Engenho Cachoeira Linda, Barreiros, PE. Detailed descriptions of survey methodology and localities surveyed are in Seipke et al. (2011).

We analyzed plumage color by comparing museum and field specimens with those of the diagnostic characters for each taxon in question. There are few museum specimens of Leptodon.
forbesi, and we complemented the analysis with data taken in the field because this taxon is critically endangered (Birdlife International 2000).

We examined the distribution of L. cayanensis for discontinuities in characters along its geographic distribution and with L. forbesi. The subspecies described by Swann (1922) and taxa considered by Hellmayr and Conover (1949) may be considered valid if at least one character does not overlap between populations (evidence of lineage divergence).

Morphometry.—We measured: beak length (from the tip to the rostral edge of the cere), width (measured at the rostral edge of the cere), wing (chord), tail length, and length (measured at 3 places at the middle of each vane and at the rachis) of the distal white and black tail bands, both dorsally and ventrally. We used analysis of variance (ANOVA) to compare morphological measurements among subspecies based on specimen locality. We used only adult male specimens to avoid possible complications due to sexual dimorphism and development, and analyzed only specimens with information describing collecting location. Coordinates, when absent, were obtained from maps. We used regression analysis to test for latitudinal trends in body size.

RESULTS AND DISCUSSION

Examination of Museum Specimens.—A specimen (MZUSP 38922) of the White-necked Hawk (Leucopternis lacernulatus) collected in 1957 in a forest fragment at Usina Sinimbu, southeastern Alagoas (Pinto and Camargo 1961) was recognized as a representative of genus Leptodon. Generic identification was based on tail and tarsi size and proportion, and morphology of the beak. The bird agrees well with the holotype of L. forbesi in all characters traditionally recognized, including the whitish hind collar, white tips on mantle feathers, scapulars, secondaries, and inner primaries, a single broad ashy-white band on the tail, and white underwing coverts. It has a white leading edge of the wings and two waves of primary molt indicating it is an adult (Edelstam 1984, Clark 2004). This specimen is now identified as L. forbesi. Recent raptor surveys failed to detect L. lacernulatus in the states of Alagoas and Pernambuco (Silveira et al. 2003, Seipke et al. 2011).

Variability in Leptodon cayanensis.—Analysis of the 71 adult Leptodon cayanensis specimens ranging from Mexico through Central America to southern Brazil and Bolivia revealed no color differences to support the subspecies described by Swann (1922). Characters supposedly diagnostic for each subspecies were found on specimens of different subspecies.

Morphometry.—Wing length of Leptodon cayanensis was more strongly associated with latitude ($r^2 = 0.38$, $F_{1,65} = 41.4$, $P < 0.05$) than was tail length ($r^2 = 0.28$, $F_{1,65} = 27.2$, $P < 0.05$; Fig. 1). The residuals for wing length and tail length were similar among all subspecies ($F_{2,63} = 2.72$, $P > 0.05$ and $F_{2,61} = 0.17$, $P > 0.05$, respectively) when controlling for this latitudinal cline. There was no relation with latitude in beak measurements (culmen and width) (both $P > 0.10$). Measurements of these characters were similar among all putative subspecies (all $P > 0.10$) and provide no support for separation of subspecies.

Distal tail bands, both black and white, were variable among the putative subspecies, while the white tail bands of L. forbesi were greater (56–57 mm) in width. The sample size for L. forbesi was small, and we described only the comparisons between the putative subspecies.
recorded in Alagoas, Brazil in October 2007. (A). Perched exposed on tree after aerial display. Note white tips to feathers on mantle, back, secondaries, and primaries (Photograph by Sergio Seipke). (B) Soaring. Note white underwing coverts, boldly patterned primaries contrasting with rest of underwing and bulging secondaries on trailing edge of wings. This bird had a dark base of the tail and only one subterminal black tail band (Photograph by Sergio Seipke).

Ventral black tail bands were similar among all the putative subspecies ($F_{3,93} = 1.32, P > 0.10$) and the remaining tail bands varied somewhat between the subspecies. *L. c. mexicanus* has narrower ventral white tail bands (25.0 mm, 15.23–44.98 mm) than the other two subspecies (*L. c. monachus* = 34.6 mm, 14.12–63.62 mm; *L. c. cayamenstis* = 31.5 mm, 10.43–48.33 mm). This relationship explained little of the variance among subspecies ($r^2 = 0.14, F_{3,85} = 5.83, P < 0.05$). The dorsal black band was greater for *L. c. mexicanus* (49.3 mm, 26.35–66.83 mm) than for *L. c. cayamenstis* (38.6 mm, 13.37–56.33 mm, $r^2 = 0.08, F_{3,93} = 3.79, P < 0.05$). The dorsal white band was larger in *L. c. monachus* (24.2 mm, 12.4–63.6 mm) than *L. c. mexicanus* (15.4 mm, 6.82–39.18 mm, $r^2 = 0.11, F_{3,91} = 5.02, P < 0.05$). Thus, while the overlap in tail band width varied among subspecies and the difference in band width only explained between 8 and 14% of the variance in band width, we conclude that band width does not distinguish among subspecies.

Validity of *Leptodon forbesi*.—Examination of museum specimens and photographic records of 27 of the 41 individuals detected in the field surveys were convincing that the species *Leptodon forbesi* (Swann, 1922) is a valid taxon.
coverts, secondaries, and inner primaries in both the type and MZUSP specimens of *Leptodon forbesi* have conspicuous white tips which are absent in *L. cayanensis*. Photographs taken in the field survey clearly show this character in at least one wild specimen (Fig. 2A). White tips of feathers seem to wear quickly in the wild.

The holotype of *L. forbesi* has a broad distal white tail band (centrale gray in *L. cayanensis*) both dorsal and ventrally with a narrower white band hidden under the tail coverts. The gray band that separates the two white bands on the ventral side is also paler in color. The broad white band is wider in the MZUSP specimen, and on the ventral side of the tail the distal black band is narrower and discontinuous in some feathers, and the proximal black band is absent. Ten of the *L. forbesi* recorded in the field had one distal and one proximal black band and one white band on the upper side of the tail, while four had a third, medial black band and two white bands. Six individuals had a single distal black band on the underside of the tail (Fig. 2B), while 13 had one distal and one medial black band. It is difficult to see the proximal tail bands in the field, as they are usually hidden under the tail coverts. We recorded one juvenile molting into adult plumage with three visible dark bands in the undertail. The tail bands in *L. forbesi* are white, and those in *L. cayanensis* are pale gray.

**Bar Part.**—Beak black. Cere and eye-ring color varies from ashy gray to a lighter pale pearl gray. Eyes dark. Tarsi show yellowish to gray color.

**Distribution.**—Recent museum specimens of *Leptodon forbesi* were collected in the eastern part of the State of Alagoas in northeastern Brazil (Fig. 3) in Sinimbu, Murici, and São Miguel dos Campos (Teixeira et al. 1987a). We found *L. forbesi* in all localities surveyed (Fig. 3). Additional surveys in the forests north and south of the sampled areas, including the states of Paraíba, Sergipe, and Bahia are needed to ascertain the distribution limits of *L. forbesi* and *L. cayanensis*.

**Habitat.**—*Leptodon forbesi* occurs in lowland and highland (0 to 585 m) Atlantic Forest. Birds have been observed soaring over open country (sugar cane fields), when moving between forest fragments, but otherwise appear to avoid such areas. Birds were also recorded flying over mangroves (*Rhizophora* spp.).

**Behavior and Ecology.**—We gathered life-history information on *L. forbesi* during field surveys in Alagoas and Pernambuco. Most birds were detected between 1 and 2 hrs after sunrise, for periods not longer than 30 min, when they soared over the forest. These kites frequently flew in pairs in October 2007 and November 2008, using the *Butterfly Display* flight (Thorstrom 1997). This behavior is best known for *L. cayanensis* and is an indicator of reproductive activity. We recorded feeding once, when a distant perched bird flew down, then returned to the same perch seconds later, and began to eat its prey. Prey identification was not possible, even using a telescope. Detection frequency in February 2008 was lower and display flights were rare suggesting the breeding season had ended. No nests or juveniles were recorded in either survey.

**Voice.**—Vocalizations of the White-collared Kite heard during field surveys apparently show no meaningful differences from known Grey-headed Kite calls. Mostly heard was the wuh-wuh-wuh..., or caw-caw-caw..., in series of 10–20, in flight, which may elicit response from individuals of nearby territories. We also heard the cat-like eeyeAAW, often during the *Butterfly Display* flight (Thorstrom 1997). Conclusions on the vocal repertoire of these species should be viewed as preliminary, despite this apparent similarity, until several better quality vocalization recordings are made, allowing comparative sonogram analysis.

**Subspecific Review of Grey-headed Kite.**—Plumage color patterns are quite variable within and among subspecies and do not follow the geographic patterns that would allow delineation of the subspecies as proposed by Swann (1922, 1945), which was also noted by Hellmayr and Conover (1949). This variation should be considered as variation among individuals within species, as is common in the Family Accipitridae (Grossman and Hamlett 1964, Brown and Amadon 1968, Thiollay 1994, Ferguson-Lees and Christie 2001).

The morphometric variation analysis shows that wing length and tail length follow Bergmann’s Rule (Fig. 1). Although restricted to wing and tail, this might explain the greater size of the southern populations of *L. cayanensis* as described by Hellmayr and Conover (1949). No significant variation was found, when controlled for latitude, to justify separating the subspecies, including the beak variables (culmen and width, which did not require correction for latitude). Tail band width variations also do not support the subspecies described by Swann (1922) for *L. cayanensis*. The
analysis revealed a slight tendency for northern populations to have a darker tail (more extensive black bands) than birds from the rest of the distribution; this has gone unnoticed in traditional morphological analysis of this species (including the present study).

**Taxonomy of White-collared Kite.**—*Leptodon forbesi* is a valid species and should be recognized. However, its diagnostic characters must be redefined in light of the new evidence. The two specimens of *L. forbesi* (type and MZUSP) as well as the three from the MN (Teixeira et al. 1987: 153) and 22 of 27 (81.5%) individuals recorded by us in the field have all-white coloration of the underwing coverts, (Fig. 2B), differing from the black of *L. cayamensis*. One individual had the greater coverts and carpal patches black on an otherwise white underwing; another had only the greater coverts black, the rest white; and one bird had a mostly white underwing with two brown areas in the proximal half of each wing; this was a juvenile molting to adult plumage. Dark coloration in the underwing of *L. forbesi* specimens should not be considered a constant in the adult plumage of this species. The character ‘coloration on the underwing coverts’ can still be recognized as a diagnosis for the taxa in question with *L. cayamensis* presenting all or most feathers black in this region.

The two specimens of *L. forbesi* (type and MZUSP) and 13 of 17, (76%) birds observed in the field showed noticeable white coloration on the leading edge of the wing, while four (24%) of the individuals observed in the field had incon-
spicuously black color in this region. Additionally, one *L. cayanensis* (MZUSP 22067) from Lago do Baptista, Amazonas State, shows extensive white lesser upperwing coverts, a plumage feature that probably rendered a white leading edge to the wings while the birds was alive. Due to the considerable variation in this character, it should not be considered a diagnosis for the taxa in question.

The character that gives *L. forbesi* its popular name, the white collar, instead of gray as in *L. cayanensis*, occurs in all specimens in the museum and in the field (Fig. 2A). This character can also be considered diagnostic, as all specimens of *L. cayanensis* examined had gray collars.

The tips of the scapulars, mantle, and wing quills are white in museum specimens and in at least one of the individuals observed in the field (Fig. 2A). This pattern is lacking in all of the specimens of *L. cayanensis*. Due to the lack of data resulting from the difficulty in assessing this character in wild specimens, and the scarcity of museum specimens of *L. forbesi*, more evidence is needed to clarify its use.

The broad white band on the tail has probably been considered the most important character for identification of *L. forbesi*, being the easiest to recognize in the field (Fig. 2B). However, we found this broad white band, although occurring in the type and in the MZUSP specimens, is absent in some individuals observed in the field. We also saw four reproductive pairs in the field for which one of the birds had a broad white band, while the others had two smaller white bands separated by a black band. This suggests the character is not diagnostic and possibly associated to sexual dimorphism in tail pattern.

Color pattern in the under surface of the remiges is also informative. Both primaries and secondaries in adult *L. cayanensis* have conspicuous black barring with narrower bars on the secondaries. The bars in adult *L. forbesi* are reduced on the secondaries and, in some cases, appear almost entirely white (Fig. 2B). Thirteen of 19 birds observed in the field, for which this barring was seen, had highly contrasting barring on primaries and secondaries, four had less contrasting patterns, and two had rather non-contrasted patterns on primaries and secondaries. This character should be considered diagnostic for species of the genus *Leptodon* despite the variation encountered in *L. forbesi*.

**Status and Conservation.**—The Atlantic Forest in northeastern Brazil is critically endangered (Ribeiro et al. 2009) with a large percentage of its original extent already destroyed and the remaining forests highly fragmented and impacted by hunting and logging. However, we found *Leptodon forbesi* in every location that we sampled (Seipke et al. 2011). Further studies are needed to estimate population density, habitat availability, and reproductive success to better understand the conservation status of this species.

**Distribution of White-collared Kite.**—Most of the literature describes the range of *L. cayanensis* extending throughout tropical humid Central and South America (e.g., Thiollay 1994, Stotz et al. 1996, Ferguson-Lees and Christie 2001), an area that includes the narrow northern section of the Atlantic Forest where *L. forbesi* occurs (eastern Alagoas and Pernambuco states, northeastern Brazil). However, the only *Leptodon* specimens found in the collections from that region are White-collared Kites. Further, no Grey-headed Kites were observed during extensive field surveys in the area (Seipke et al. 2011). Redefinition of the diagnosis for both species suggests that many if not all of the previous Grey-headed Kite records in the White-collared Kite’s range, most of which are not documented by either photographs or specimens, are doubtful at the least, and that probably both species are allopatric. Grey-headed Kite records from the immediate south of this area (Sergipe and northern Bahia states) lacking documentation should also be viewed with caution. Whether the White-collared Kite’s range extends as far south as northern Bahia remains to be verified as new records arise, based on the precise field identification data available (Seipke et al. 2011). However, southern Bahia is apparently within Grey-headed Kite range, as exemplified by two MZUSP specimens from Ilhéus and many documented records (LFS, pers. obs.).

Uncertainty still exist in details of the life history of the White-collared Kite, including juvenile color patterns and geographic distribution among others, but recognizing this species as valid is important. Its validation will pave the way for future studies of its natural history, morphology, population dynamics, biogeography, genetic structure as well as help examine its status as a threatened species.

**ACKNOWLEDGMENTS**

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LITERATURE CITED


APPENDIX

Specimens

Leptodon forbesi = 2.

BRAZIL: “Pernambuco” — no specific locality (NHM: 1 unsexed); Alagoas: Usina Serra Branca. Murici (MNRJ: 1q; fide Teixeira et al. 1987a:153); São Miguel dos Campos (MNRJ: 1cr, 1q; fide Teixeira et al. 1987a:153).

Leptodon cyanencnis = 126.

No specific locality (NHM: 3 unsexed; MNRJ: 2q, 7 unsexed; ZMB: 2 unsexed).
BELIZE: Orange Walks (NHM: 1 unsexed); Cayo, Western District (NHM: 1♂).

BOLIVIA: Esperanza (NHM: 1♂). BRAZIL: no specific locality (ZMB: 1 unsexed); MNRJ: 1 unsexed; NHM: 1 unsexed); Roraima: Rio Jamari (MNRJ: 1 unsexed); Amazonas: Lago Camaquã (MZUSP: 1♂); Rio Jurua, Rio Eiru, Santa Cruz (MZUSP: 1♂, 1♀); Lago do Baptista (MZUSP: 1♂); PARÁ: "Pará" - no specific locality (NHM: 1 unsexed); Capim (MZUSP: 1♂); Rio Tapajós, Fordlandia (MZUSP: 2♂); Rio Tapajós, Ucurentuba (MZUSP: 1♂); Santarém (MNRJ: 2♂); Taperinhas (MZUSP: 1♀); Utinga (MZUSP: 1♂, MNRJ: 1♂); Jardim Zoológico, Belém (MNRJ: 1♂).

MATO GROSSO: no specific locality (MNRJ: 1 unsexed); Cuiabá: Vila Santo Antônio, Fazenda Marraquiss (MZUSP: 1♂); Chapada (NHM: 1♂); Serra da Chapada (NHM: 1♂); Coxipó Mirim, Cuiabá (MNRJ: 1♀). GOIÁS: Cana Brava, Nova Ronta (MZUSP: 1♂); Rio Palma (MNRJ: 1 unsexed).

BAHIA: no specific locality (ZMB: 1 unsexed); Ilhéus (MZUSP: 1♂, 1♀). MATO GROSSO DO SUL: Salobra (MZUSP: 1♂). MINAS GERAIS: Peti, Santa Bárbara (MZUSP: 1♂); Jaguaraí, Matosinhos, Rio das Velhas (MNRJ: 1 unsexed).

ESPIRITO SANTO: Pau Gigante (MZUSP: 1♂); Chaves, Santa Leopoldina (MZUSP: 1♂); Santa Cruz (MZUSP: 1♀); Santa Teresinha (MNRJ: 1♂); São Paulo: Boracéia (MZUSP: 1♂); Crystalis Franca (MZUSP: 1♂); Icaparã (MZUSP: 1 unsexed); Ilucrêva (MZUSP: 1♂); Ubatuba (MZUSP: 1♂, 1♀); São Paulo (MZUSP: 3 unsexed). RIO DE JANEIRO: Rio de Janeiro (MNRJ: 1♂, 2♀); Terezópolis (MNRJ: 1♂, 1♀).

PARANÁ: Jacarezinho (MZUSP: 1♂). SANTA CATARINA: no specific locality (MZUSP: 1♂); RIO GRANDE DO SUL: Pelotas (NHM: 1 unsexed).

COLOMBIA: Santa Martha (NHM: 1♀); Caracolitico, Magdalena (ICN: 1♀); Campo Costa, Magdalena (ICN: 1♀); Chico, Rio Jurado (ICN: 1♂); Guapi, Cauca (ICN: 1♀, 1 unsexed).

COSTA RICA: no specific locality (NHM: 2 unsexed); Nicoya (NHM: 1 unsexed).

ECUADOR: Sarayacu (NHM: 5 unsexed).

GUATEMALA: Costa Cuca (ZMB: 1♂).

GUIANA: no specific locality (ZMB: 1♂). HONDURAS: no specific locality (NHM: 1 unsexed).

MEXICO: Tampico (NHM: 1♂).

NICARAGUA: San Emilio, Lake Nicaragua (NHM: 1♂).

NICARAGUA: San Emilio, Lake Nicaragua (NHM: 1♂).

PANAMA: no specific locality (NHM: 1 unsexed); Chiriquí (NHM: 1♀, 1♀, 1 unsexed).

PERU: Chamicurco (NHM: 1♂); Nauta (NHM: 1♂).

TRINIDAD: no specific locality (NHM: 1 unsexed). VENEZUELA: Caracas (NHM: 1 unsexed); El Palmar, Bolívar (MEBRG: 1♂); El Valle, Mérida (COP: 1♂); Esteros do Camaguan, Guárico (MEBRG: 1 unsexed); Cuare, Falcón (MEBRG: 1♂); Isla Tapacana, Amazonas (COP: 1♂); Las Adjuntas, Bolívar (MEBRG: 1♂); Las Carmelitas, Amazonas (COP: 1♂); Las Quiaguas, Carabobo (COP: 1♂); Porto Cabello (NHM: 1♂, ZMB: 1♀); Río Aripacu, Zulia (MEBRG: 1♂); San Joaquín de Navay, Táchira (MEBRG: 1♂); Tivana, Falcón (MEBRG: 1♂).
INTERACTIONS OF RAPTORS AND LESSER PRAIRIE-CHICKENS AT LEKS IN THE TEXAS SOUTHERN HIGH PLAINS

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ABSTRACT.—We examined behavioral interactions of raptors, Chihuahuan Ravens (Corvus cryptoleucus), and Lesser Prairie-Chickens (Tympanuchus pallidicinctus) at leks in the Texas Southern High Plains. Northern Harriers (Circus cyaneus) and Swainson’s Hawks (Buteo swainsoni) were the most common raptors observed at leks. Only 15 of 61 raptor encounters at leks (0.09/hr) resulted in a capture attempt (0.02/hr). Mean (± SD) time for Lesser Prairie-Chickens to return to lekking behavior following a raptor encounter was 4.2 ± 5.5 min suggesting the disturbance had little influence on lekking time.

Lesser Prairie-Chicken (Tympanuchus pallidicinctus) populations have declined throughout much of their historic range (Crawford and Bolen 1976, Hagen et al. 2004). Taylor and Guthery (1980) estimated that ≥90% decrease had occurred in their occupied range since the 1800s. Currently, small populations exist in parts of Colorado, Kansas, New Mexico, Oklahoma, and Texas (Hagen and Giesen 2005). The population decline has resulted in Lesser Prairie-Chickens being designated as a candidate species by the U.S. Fish and Wildlife Service for protection under the Endangered Species Act of 1973 (USDI 2008).

Lekking species may be more susceptible to predation as they are congregated, focused on mating, and exposed (Hartzler 1974). Lehmann (1941:39) stated that “Prairie chickens on the courtship grounds seemed more intent on mating than on self-preservation; consequently, losses from predation were probably heaviest at mating time.” Wolfe et al. (2007) reported male mortality was highest during peak lekking activity and suggested the cause may be male conspicuousness and/or predators focusing on lekking activity, although they did not report how many males were actually killed on leks. Schroeder and Baydack (2001) speculated that habitat degradation at prairie grouse leks may have exacerbated predation risks. Few studies, however, have investigated predation on North American prairie grouse leks (e.g., Berger et al. 1963, Hartzler 1974, Boyko et al. 2004) and no study has specifically identified predation on leks as a major source of mortality.

Direct predation and disturbance of breeding activities may limit reproduction of birds (Cresswell 2008). Baydack and Hein (1987) reported female Sharp-tailed Grouse (T. phasianellus) avoided disturbed leks (e.g., presence of humans, dogs, vehicles, snow fences, propane exploder scarecrows, and radio noises). Alternatively, congregation of birds at leks may reduce predation risk due to increased probability of detecting a predator before it becomes a serious threat. The predation risk for each individual decreases as the number of individuals in a group increases as long as predation events do not increase as well (Boyko et al. 2004). Flushing as a group may confuse a predator and make it harder to select an individual (Lack 1968). Wittenberger 1978:1 Leks are generally in the same location year after year, possibly because they have proven to be safe in the past (Lack 1968).

Raptors have been identified as predators of Lesser Prairie-Chickens (Campbell 1950, Haukos
specific to our study area, Northern Harriers (Circus cyaneus) have been observed predating Lesser Prairie-Chickens in eastern New Mexico (Campbell 1950) and the Texas Southern High Plains (Haukos and Broda 1989). Our objectives were to examine: (1) encounter rates and incidences of raptor predation at Lesser Prairie-Chicken leks, and (2) behavioral responses of prairie-chickens to different raptor species and Chihuahuan Ravens (Corvus cryptoleucus) at leks in the Texas Southern High Plains.

METHODS

Study Area.—Our study occurred on private lands in Cochran and Yoakum counties in the Texas Southern High Plains ecoregion (Llano Estacado). The topography is flat to gently undulating with small vegetated dunes. The dominant vegetation in most areas was shinnery oak (Quercus havardii) intermixed with sand sagebrush (Artemisia filifolia) and grasses. The major land use in this area was agriculture with a high proportion of the area under intensive cultivation and cattle production. Oil development occurred throughout the study area with Yoakum County producing 23,730,647 barrels of oil in 2007 (Railroad Commission of Texas 2010).

Field Methods.—We used a combination of direct observation and video-recording to monitor raptor—Lesser Prairie-Chicken encounters at leks during spring 2007 and 2008. We used four leks known by landowners and Texas Parks and Wildlife Department staff in 2007, and included three new leks located by roadside surveys in 2008 (Behney 2009). We excluded two of the 2007 leks due to logistical constraints in 2008. Direct observations were conducted from small, camouflaged, pop-up style blinds placed among vegetation at the edge of the lek, or from a vehicle parked within 15 m of the lek. We arrived at leks before prairie-chickens were present; typically >1.5 hrs before sunrise and remained stationary for the duration of the observation period. We used binoculars and spotting scopes to monitor prairie-chickens and identify predators. We did not depart the lek until 20 min after the last prairie-chicken departed each morning.

We placed two video-recording systems at each lek being video-monitored. One system was placed sufficiently far from the lek to ensure the entire area was recorded (far) and the second system was placed close to or zoomed in (close) to record behaviors of grouse and predators. This camera arrangement was not possible on one lek and we used two camera systems placed the same distance from the lek but at different angles.

Each video-recording system consisted of a security style camera connected to a video camera recorder (VCR) or digital video camera recorder (DVDR). Camera systems were powered by a 12-volt deep-cycle marine battery connected to a power inverter, and enclosed in weatherproof housing. A power strip was connected to the inverter, into which the VCR and the security camera were connected. The VCR or DVDR recorded real-time video to facilitate identification of flying raptors and behavior of prairie-chickens.

Recording occurred 2–4 days/week at each lek. We recorded lek activities from 0.5 hrs before sunrise to 2–4 hrs post-sunrise and from 2 hrs before sunset to 0.5 hrs after sunset. All tape and battery changes were at mid-day (1100–1400 hrs) when prairie-chickens were not present to minimize risk of disturbance. We used an editing VCR to review the collected video footage of activities at leks. We initially viewed the far camera recordings to identify behaviors (predator, flushing, disturbance) and then viewed the close up tape for a more in-depth view. We reviewed both tapes completely in the case where two cameras were placed the same distance from the lek.

We noted the time, date, lek, species, age (if possible), raptor approach type, and prairie-chicken response type if a raptor or raven was observed. The raptor or raven had to be within 35 m of the lek (visually estimated) to be included in the analysis. At this distance the raptor or raven and Lesser Prairie-Chickens should have been able to see each other. We classified raptors to the lowest taxonomic level possible when we could not identify the raptor species. We pooled Peregrine Falcon (Falco peregrinus), Prairie Falcon (F. mexicanus), Merlin (F. columbarius), and unknown falcons (Falco spp.) in a “falcon” group and Red-tailed Hawk (Buteo jamaicensis), Ferruginous Hawk (B. regalis), and unknown buteos (Buteo spp.) in a “buteo” group. We pooled Cooper’s Hawks (Accipiter cooperii) and Sharp-shinned Hawks (A. striatus) into an “ac-cipiter” group.

Statistical Analysis.—Raptor approach types were classified as predation attempt, course, perch, or fly-by. “Predation attempts” were obvious dives at or chases of Lesser Prairie-
Chickens. "Coursing" was a low, slow glide over the landscape in search of prey, typical of Northern Harriers. "Perch" was noted any time a raptor landed in view of the camera, and a "fly-by" was when the raptor paid no apparent attention to prairie-chickens as it flew over. Responses of prairie-chickens to raptors and ravens were categorized as no response, squat, partial flush, or flush. We considered a raptor/raven-prairie-chicken encounter as eliciting "no response" if we could not observe any alteration in behavior of the grouse when the encounter occurred. "Squat" consisted of seeking cover or flattening against the ground. "Partial flush" consisted of at least one but not all prairie-chickens flushing from the lek, and "flush" occurred when every grouse on the lek flushed.

We noted the time when lekking behavior ceased to when at least two Lesser Prairie-Chickens returned to lekking behavior. Raptor encounter rates were calculated by dividing the number of raptors observed at leks by the hours of lek observation or recording during which prairie-chickens were present. We used an exact rate ratio test assuming Poisson counts in Program R to compare raptor encounter rates (R Development Core Team 2008, Fay 2009).

We used a G-test for goodness of fit to compare frequency of occurrence of different raptor species observed at leks to the overall raptor community in the area following Sokal and Rohlf (1995). We used frequency of occurrence at leks by Swainson’s Hawks, Northern Harriers, falcon species, and buteo species (not including Swainson’s Hawks) as observed values. Expected values were computed from data collected during standardized raptor surveys in the area (Behney 2009). Only surveys conducted during February, March, and April were included and were pooled over years. The total number of each raptor species or species group observed during surveys was divided by the total number of all raptors recorded during surveys. We then multiplied this proportion by the total number of raptors observed at leks to sum to the same total as raptors seen at leks, while maintaining the same proportion of each species/species group.

We used Chi-square tests of independence (Conover 1999) to assess independence among approach, species, and response. We also used a Chi-square test to assess differences in behavioral response of Lesser Prairie-Chickens to raptor encounters compared to raven encounters. We used a Kruskall-Wallis test (Conover 1999) to compare prairie-chickens return times associated with different raptor species because the data were not normally distributed. We categorized the lekking season into five 2-week intervals to assess temporal variations in encounter rates and species dynamics: 1 = 9 to 22 March, 2 = 23 March to 5 April, 3 = 6 to 19 April, 4 = 20 April to 3 May, and 5 = 4 to 17 May.

**RESULTS**

**Raptor Encounter Rates.** —We conducted 155 hrs of direct observation at seven leks while Lesser Prairie-Chickens were present between 24 February and 21 May 2007 and 2008. We observed 21 ravens and 37 ravens on or near leks while prairie-chickens were present. We recorded 495 hrs of real-time video footage on seven leks while prairie-chickens were present from 3 April through 9 June 2007 and 8 March through 22 May 2008. We observed 40 raptors and 104 ravens on or near leks while prairie-chickens were present during the video recordings.

There was no difference in encounter rates between viewing platform (direct observations = 0.14 raptors/hr, video = 0.08 raptors/hr; \( P = 0.08 \)) and the data were pooled (overall = 0.09 raptors/hr). Study leks averaged 12.3 males (range = 6–19). We did not observe any successful predation events on the video or through direct observations.

Northern Harriers (\( n = 30 \)) were the most commonly observed raptor at leks followed by Swainson’s Hawks (\( n = 11 \)), other buteos (\( n = 9 \)), falcons (\( n = 5 \)), and accipiters (\( n = 2 \)). We were unable to identify five raptors to the genus level.

We observed one additional Peregrine Falcon encounter at a lek during direct observations but failed to note the time Lesser Prairie-Chickens departed the lek and were unable to assess the duration of lek attendance by prairie-chickens that morning. This encounter was included in behavioral analyses but not in encounter rate calculations. Encounter rates peaked during the second 2-week period and steadily decreased to their lowest rates during the last interval (Fig. 1). Proportions of individual raptor species or species groups at leks diverged from that expected based on the observed raptor community (\( \chi^2 = 45.4; P < 0.001 \)). More Northern Harriers (contribution to overall G-statistic = 28.92), fewer Swainson’s Hawks (−12.08), and more falcons (8.20) were observed at leks than expected based on the raptor community present in the area.
FIG. 1. Species and species group-specific raptor encounter rates (birds/hr) and female Lesser Prairie-Chicken visitation rate (females/day) for 2-week intervals throughout the lekking season in the Texas Southern High Plains, 2007–2008. Two-week interval start dates were: 1 = 9 March, 2 = 23 March, 3 = 6 April, 4 = 20 April, and 5 = 4 May.

**Raptor Approach Types.**—Coursing was the most commonly observed approach type (44% of encounters) used by raptors, followed by perching (24%), fly by (16%), and predation attempt (16%). We detected 15 predation attempts on Lesser Prairie-Chickens, primarily by Northern Harriers (n = 7), Swainson’s Hawks (n = 3), and falcons (n = 2). Accipiters, other buteos, and unknown raptors accounted for one predation attempt each. Northern Harriers were the most common raptor observed coursing whereas buteo hawks were more commonly seen perching. Approach type was related to raptor species ($X^2 = 17.25, P = 0.008$). Northern Harriers perched less than expected. Swainson’s Hawks attempted to prey upon prairie-chickens more than expected, and other buteos perched more than expected.

**Lesser Prairie-Chicken Response Types.**—Some or all Lesser Prairie-Chickens flushed in 62% of all raptor encounters. However, prairie-chicken response was associated with raptor type (Northern Harrier, buteo, or falcon; $X^2 = 14.5, P = 0.02$). Harriers and buteos were more likely to elicit flushing responses (75 and 73% of all responses, respectively). In contrast, three of five falcon encounters elicited squat responses from prairie-chickens (Fig. 2). This is likely a low estimate because flushes often occurred only after

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**FIG. 2.** Lesser Prairie-Chicken response to Northern Harriers (n = 30), buteos (including Swainson’s Hawks, n = 20), and falcons (n = 5) encountered at leks in the Texas Southern High Plains, 2007–2008.
falconsb repeatedly dove at prairie-chickens. The initial response in all falcon encounters was for prairie-chickens to squat and stay on the ground; however, after repeated swoops by the falcon, a few eventually flushed in two encounters and were recorded as partial flushes.

Lesser Prairie-Chickens are apparently able to differentiate risk posed by different avian predators and respond accordingly. Raptors elicited some type of response in 85% of encounters whereas only 9% of raven encounters elicited a response (X² = 138, P < 0.001). Mean ± SD time for at least two prairie-chickens to be displaying at leks following a raptor encounter was 4.22 ± 5.5 min. Return times were different following encounters involving different raptor species (Kruskal-Wallis Rank Sum Test, X² = 11.895, P = 0.036; Fig. 3).

**DISCUSSION**

Sage- and prairie grouse spend a substantial amount of time on leks (typically 3–4 hrs/day, Hagen and Giesen 2005) during the spring. Their congregation and exposure could lead to increased predation risk (Lehmann 1941, Hartzler 1974, Schroeder and Baydack 2001). Our data suggest raptor predation on Lesser Prairie-Chickens at leks is uncommon. We did not observe any successful predation events at leks despite 650 hrs of data from when Lesser Prairie-Chickens were on leks.

Our results are similar to those from other studies of lekking species as successful predation events on leks were rare or absent (Berger et al. 1963, Moran 1966, Haukos and Broda 1989). Encounters classified as predation attempts in our study were rare (0.02 attempts/hr). This suggests use of a lek mating system may limit predation events and may be an efficient anti-predator strategy (Boyko et al. 2004).

Northern Harrier encounters peaked during the 2-week interval of 23 March to 5 April, after which they began migrating from the study area (Fig. 1; Behney 2009). Buteoine hawk encounters were low throughout the lekking season but peaked during the interval starting 6 April, which corresponded to migrants moving through the area while some wintering hawks were still present (Behney 2009, Preston and Beane 2009). Swainson's Hawk encounters were low throughout the season but peaked during the interval starting 1 April. This corresponded to arrival of Swainson's Hawks migrating from the southern hemisphere (England et al. 1997, Behney 2009) and establishment of breeding territories in the study area. The period of peak female attendance at leks corresponded to dramatic decreases in raptor encounters at leks (Fig. 1). Haukos (1988) reported a similar observation that peak female Lesser Prairie-Chicken attendance at leks occurred just after most raptors had migrated through the area.

Lesser Prairie-Chicken responses to predation attempts appear to correspond to the hunting strategies of different raptor species. Northern Harriers and buteo hawks (including Swainson's.
Hawks) typically capture prey on the ground and would likely have difficulty overtaking and catching a prairie-chicken in the air (Macwhirter and Bildstein 1996, England et al. 1997). These raptor species elicited more flushing responses from prairie-chickens. Falcons evolved to overtake and capture prey in the air (Webster 1944, White 1962), and elicited more of a squatting response and an observable hesitancy to flush by prairie-chickens. This suggests Lesser Prairie-Chickens are able to assess the threat posed by different raptor species and have evolved the appropriate behavioral response.

We are confident we detected all raptor predation attempts on Lesser Prairie-Chickens at leks during monitoring and video-recording periods. However, it is possible that we missed some raptor fly-bys or coursing that occurred behind or over the blind or camera. We believe any observer effect on raptor presence or behavior was minimal due to the small size of the blind, our arrival well before sunrise, and that we remained stationary throughout the observation period. Encounter rates were higher for direct observation than video-recording, suggesting observer presence was not inhibiting raptor presence.

Raptors were not a source of mortality or marked disturbance of Lesser Prairie-Chickens while on leks in our study. This suggests mortality of lekking Lesser Prairie-Chickens from raptor predation is not a factor contributing to population declines.

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LITERATURE CITED


GEOGRAPHIC VARIATION IN TYPE I SONGS OF BLACK-THROATED GRAY WARBLERS

STEWART W. JANES1,2 AND LEE RYKER1

ABSTRACT.—We studied songs of Black-throated Gray Warblers (Dendroica nigrescens) in a fragmented landscape in southwestern Oregon and northern California where each male sings a single Type I song consisting of two phrases. Fourteen variants of Type I songs were distributed in a complex geographic pattern across 19,400 km² of the region. Variants differed in number of notes/syllables in the A-phrase (range 2–5), and the B-phrase differed in both the number and structure of syllables. Several variants occurred in well-defined areas and differed from neighboring songs; others overlapped adjacent variants or graded from one form to another across a narrow zone. Distinct variants could be identified, but the diversity of Type I songs and the pattern of distribution throughout the region does not describe a clear system of dialects. Geographic extent of the variants differed considerably; some occurred as small scattered populations occupying <250 km² while the largest exceeded 3,000 km². Variants in the most restricted area and having the most fragmented distribution had the least consistent structure among individuals both within local populations and across the range of the variant. Ridges >1,000–1,200 m in elevation served as effective barriers and separated sets of similar song variants. Fire also likely had a role in generation of variants as reflected by multiple variants occurring in areas lacking obvious geographic barriers. Received 8 December 2009. Accepted 23 December 2010.

The songs of most birds exhibit geographic variation. This variation may be manifested as dialects: songs similar in form, distinct from neighboring song variants, and exhibiting minimal spatial overlap with neighboring song variants.

Many species of wood-warblers (Parulidae) sing multiple distinct songs that can be classified into two general song categories (Spector 1992) on the basis of context. Type I songs predominate early in the breeding season prior to pairing. Type II songs tend to be delivered before dawn after pairing, near territorial boundaries, during territorial contests, and often with chip-like notes. Songs of the two categories often differ in structure and are termed form-encoded songs (Byers 1995). Dialects are common among second category songs of wood-warblers with form-encoded songs, but not among first. Chestnut-sided Warblers (Dendroica pensylvanica), for example, exhibit dialects of Type II (second category) songs that change over a distance of several kilometers but sing similar Type I (first category) songs from Minnesota to Massachusetts, a distance of 1,600 km (Byers 1996).

The Hermit Warbler (D. occidentalis) is one of the few wood-warblers for which dialects of Type I songs have been described (Janes and Ryker 2006). The dialects encompass relatively large areas at times exceeding 6,000 km², much larger areas than dialects of Type II songs by other wood-warblers. The spatial scale of Type I dialects among Hermit Warblers is similar to that of dialects observed in other species such as White-crowned Sparrows (Zonotrichia leucophrys) (Chilton and Lein 1996, Nelson and Soha 2004).

Black-throated Gray Warblers (D. nigrescens) breed in the same fragmented landscape as Hermit Warblers and also sing form-encoded songs (Morrison and Hardy 1983, Morrison 1990, Guzy and Lowther 1997). We investigated whether Black-throated Gray Warblers exhibit dialects of Type I songs and whether song differences are similar to those of Hermit Warblers in differentiation and geographic pattern and scale.

METHODS

Study Area.—The area encompassed 19,400 km² in southern Oregon and northern California from the coast to the Cascade Mountains, and from the Klamath River watershed north to the Umpqua River watershed (Fig. 1). The natural vegetation of the area is diverse including grassland, chaparral, oak (Quercus garryana) savanna, and a variety of forest types (Franklin and Dymess 1973). Black-throated Gray Warblers tend to occur at lower elevations within the study area. They are most common in the interior valleys in the interface between (1) chaparral dominated by buckbrush (Ceanothus cuneatus), whiteleaf manzanita (Arctostaphylos vicina), and poison oak (Toxicodendron diversiloba), (2) Oregon white oak (Q. garryana) woodland, and (3) mixed conifer/hardwood forest dominated by Douglas-fir (Pseudotsuga menziesii), Pacific madrone

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(Arbutus menziesii), and California black oak (Q. kelloggii). They attain their highest abundance in areas where canyon live oak (Q. chrysolepis) is most common and are less abundant or absent in riparian areas where white alder (Alnus rhombifolia) and bigleaf maple (Acer macrophyllum) are common. They occur most often in riparian areas along the coast dominated by red alder (A. rubra) and bigleaf maple.

Data Collection and Analysis.—We distinguished Type I and II songs of Black-throated Gray Warblers based on the context in which they were delivered (Specter 1992). Use of Type I and Type II songs by Black-throated Gray Warblers in distinct contexts coincides with that of other wood-warblers with form-encoded songs.

We systematically searched the accessible roads in appropriate habitat between 1998 and 2007 recording Type I songs of Black-throated Gray Warblers with a Sony TCD5 Proll cassette recorder coupled with a Sennheiser ME-62 microphone in a 61-cm parabolic reflector until 2004. We used a Marantz PMD660 recorder beginning in 2004 coupled with a Sennheiser ME-62 microphone in a 61-cm parabolic reflector. Type I songs were recorded between 16 April and 4 July each year with most sampled between sunrise and the attenuation of singing about 1100
RESULTS

Song Variants and Dialects.—Type I songs of 315 Black-throated Gray Warblers recorded in southwestern Oregon and northern California over a period of 10 years exhibited considerable geographic variation. Fourteen variants of Type I song were identified (Fig. 3). We use the term 'variant' to include both dialects and songs that do not meet the strict definition of a dialect because their distribution either substantially overlapped the geographic range of another variant or transitional songs changed rapidly in structure across a narrow zone between two variants. We identify the variants by an associated geographic feature for convenience.

Five variants met the definition of a dialect: Applegate, Days, Humbug, Agness, and Winchuck. Songs were discrete, and the geographic range of each exhibited little or no overlap with adjacent variants. Males singing these variants were rarely encountered outside the boundaries of the mapped area. Only two individuals singing Applegate dialect, two singing the Days dialect, and one singing the Agness dialect were encountered >5 km from the mapped area.

Variants broadly overlapped in space at other locations. This was most obvious among several occupying the most restricted areas. Cow and Starvout variants each occupied a limited geographic area, and the distribution of each broadly overlapped the other as well as the neighboring Grave variant (Fig. 1). Nowhere in their ranges were these two variants common.

The Crooks variant occupied two relatively small areas embedded within the area occupied by the Caves variant. The Crooks variant occurred in the absence of the Caves variant in only three small disjunct watersheds. In addition, a relatively large number of males (n = 8) were recorded singing the Crooks variant at distances of 14–41 km from the mapped area of this variant and within other variant areas.

Other variants failed to meet the strict definition of a dialect because the structure of the song was not discrete. An area of transition between the Caves and Grave variants was identified. Individuals delivered songs intermediate in form in small, isolated populations across a 15-km wide zone. Each variant beyond this transition zone was consistent with respect to the unique features of the respective songs.

Variation in song was observed among individuals of some variants (Fig. 4). The tonal note in the first phrase for about half the individuals singing the Caves song, for example, consisted of a single note delivered at a nearly constant frequency. The tonal note in others varied in frequency resulting in two maxima. The tonal notes in the songs of still other individuals became two distinct notes, each increasing in frequency. This variation occurred throughout the range of the Caves variant, but the double-tonal note form was most common in the southern part of the range. A similar pattern of both single and double tonal notes in the first phrase was also noted within the Agness variant.

Song Structure.—All Type I songs in the study area regardless of variant were composed of two phrases (Fig. 2). The A-phase consisted of a series of repeated multi-note syllables, each including one vibrato note and 1–4 tonal notes. The bandwidth of the vibrato notes in the Crooks and Emigrant variants was narrow in most songs,
approaching a tonal note. The B-phrase consisted of 2-5 syllables in all variants, most differing in form, frequency, and duration.

Variants in the upper Rogue River watershed in the large central part of the study area were arbitrarily chosen as a basis for describing the B-phrase and in making comparisons with other variants. The B-phrase of songs in the upper Rogue River watershed shared a common five-syllable pattern (Fig. 2). The occurrence of these or similar syllables varied among each of the variants (Table 1).

The first syllable of the B-phrase (B₁) was relatively long in duration and relatively low in frequency compared to other syllables in the song. For most it included a brief introductory tonal note. A second tonal note was often appended to the end of the vibrato note. The vibrato note in some variants (Grave and Emigrant) was reduced to a tonal note in most individuals.

B₂ and B₃ were similar in form, frequency, and duration. The most common form of the syllable began with a vibrato note of relatively high frequency coupled with a tonal note of constant or decreasing frequency. We also observed paired syllables similar to B₂ and B₃ in songs north of the study area into the northern Oregon Coast Range. Oregon Cascades east and west of the divide, and

FIG. 4. Examples of Type I songs of four different male Black-throated Gray Warblers from each of four variants in southwestern Oregon and northern California illustrating variation within variants, 1998–2007. The variants are (A) Applegate and (B) Grave, relatively large and continuous populations; (C) Emigrant, a small (2 km²) isolated population; and (D) Diamond Rock, a highly fragmented population.

central Washington, although not in all variants. B₂ and B₃ tended to fuse in some variants into a single syllable.

B₄ consisted of a single vibrato or tonal note delivered at a relatively high frequency, the highest in a song. B₄ began with a tonal note that decreased in frequency often ending with a vibrato note of relatively low frequency, typically the lowest in a song.

This pattern or some derivative characterized the B-phrase of nine of the 14 variants, but variants in the southern and western portions of the study area did not conform well to this model. Some of the syllables in the B-phrase may be modified forms of B₁–₃, but the relationships are not clear (Fig. 3, Table 1).

Relations Among Song Variants.—Some variants had close affinities based on structure. In particular, variants from the upper Rogue River watershed (Applegate, Caves, Crooks, Grave, Diamond Rock, and Emigrant) comprised one set of variants. Syllables from the A-phrase typically included a vibrato note followed immediately by one or two tonal notes in addition to similarities in structure of the B-phrase. The order of vibrato and tonal notes was reversed in the Grave population.

Variants outside the upper Rogue River watershed differed although conforming to the same
Table 1. Structure of Black-throated Gray Warbler Type I songs in southwestern Oregon and northern California. The occurrence of B-phrase syllables represents the percentage of songs in which the syllable was present. Brackets indicate the two adjacent syllables combine into a single syllable in >50% of the songs in the song form. A question mark indicates the occurrence of a syllable but whose relationship to B, 5 from the Upper Rogue Valley variants is uncertain.

<table>
<thead>
<tr>
<th>Watershed/region</th>
<th>Song variant</th>
<th>n</th>
<th>Sequence of notes in A-phrase syllable</th>
<th>% occurrence of B-phrase syllables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>B₁ B₂ B₃ B₄ B₅</td>
</tr>
<tr>
<td>Upper Rogue River</td>
<td>Emigrant</td>
<td>6</td>
<td>VT</td>
<td>50 [100] 100 83 33</td>
</tr>
<tr>
<td></td>
<td>Applegate</td>
<td>147</td>
<td>VT</td>
<td>99 99 97 99 81</td>
</tr>
<tr>
<td></td>
<td>Caves</td>
<td>103</td>
<td>VT, VTT</td>
<td>79 99 75 99 66</td>
</tr>
<tr>
<td></td>
<td>Grave</td>
<td>59</td>
<td>TV</td>
<td>100 100 100 88 88</td>
</tr>
<tr>
<td></td>
<td>Crooks</td>
<td>44</td>
<td>VTT</td>
<td>100 100 98 100 100</td>
</tr>
<tr>
<td></td>
<td>Diamond Rock</td>
<td>12</td>
<td>VTT</td>
<td>25 25 [83] 83</td>
</tr>
<tr>
<td>Upper Umpqua River</td>
<td>Cow</td>
<td>6</td>
<td>TV</td>
<td>93 100 50</td>
</tr>
<tr>
<td></td>
<td>Starvout</td>
<td>11</td>
<td>TTVT</td>
<td>218 27 [73] 73</td>
</tr>
<tr>
<td></td>
<td>Days</td>
<td>27</td>
<td>VTTT, TVTT</td>
<td>100 93 93 78</td>
</tr>
<tr>
<td>Klamath River</td>
<td>Humbug</td>
<td>28</td>
<td>TTVT, TVTT</td>
<td>786 [789] 782 [96] 79</td>
</tr>
<tr>
<td></td>
<td>Happy Camp</td>
<td>3</td>
<td>VT</td>
<td>?100 ?100 [100] 100</td>
</tr>
<tr>
<td>Coast</td>
<td>Agness</td>
<td>11</td>
<td>VT, VTT</td>
<td>91 291 64</td>
</tr>
<tr>
<td></td>
<td>Winchuck</td>
<td>17</td>
<td>TVT</td>
<td>?88 [100] 100 100</td>
</tr>
<tr>
<td></td>
<td>Smith</td>
<td>3</td>
<td>TVT</td>
<td>267 [767] 100 67</td>
</tr>
</tbody>
</table>

* V = vibralo note, T = tonal note.

General pattern (2 phrases with the first phrase composed of repeated syllables including 1 vibrato note). However, syllables of the first phrase often differed in notable ways, especially in the Days dialect of the Umpqua River watershed to the north (Fig. 3). This characteristic syllable or a variation thereof occurred at least as far north as Gales Creek in the northern Oregon Coast Range and into central Washington. However, not every variant sampled in this area incorporated this or a related syllable.

Relationships among variants along the coast and the Klamath River were less clear. Coastal variants (Winchuck and Smith) shared similar syllables in the A-phrase, and the Winchuck and Humbug variants from the Klamath River shared similarities in structure of the B-phrase, but the four variants do not form a clearly related set. The Agness variant between the Upper Rogue River set of variants and the Winchuck variant on the coast shared some similarities with both.

Distribution and Stability of Variants.—The geographic limits of related variants corresponded to ridges 1,000-1,200 m or greater in elevation above mean sea level. The Siskiyou Mountains oriented east-west along the Oregon-California border formed one boundary. The Kalmiopsis and Coast Range oriented north-south formed another, separating coastal variants from those of the interior valleys. Apparently suitable habitat occurred along the Illinois and Rogue river canyons that transect the coastal mountains. However, variants did not tend to extend through these narrow corridors.

Ridges 700-1,000 m in elevation served as partial barriers for the Agness, Caves, and Grave variants with limited distribution extending across these ridges. Boundaries of variants within the regions defined by these ridges did not conform to obvious geographic features.

Song variation was greatest in the most fragmented and geographically limited variants. For example, the restricted and isolated Emigrant variant included considerable variation among the neighboring males (Fig. 4D).

The Diamond Rock song varied across its fragmented range, barely qualifying as a distinct song (Fig. 4C). Syllables of the A-phrase exhibited clinal changes across the long axis of the range, becoming more similar to the Caves variant.
TABLE 2. Geographic extent of the Type I song forms of Black-throated Gray Warblers in southwestern Oregon and northern California. Numbers in parentheses indicate song variant areas whose complete distributions are undescribed.

<table>
<thead>
<tr>
<th>Song variant</th>
<th>Area (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emigrant</td>
<td>2</td>
</tr>
<tr>
<td>Applegate</td>
<td>472</td>
</tr>
<tr>
<td>Caves</td>
<td>1,634</td>
</tr>
<tr>
<td>Crooks</td>
<td>209</td>
</tr>
<tr>
<td>Grave</td>
<td>503</td>
</tr>
<tr>
<td>Diamond Rock</td>
<td>107</td>
</tr>
<tr>
<td>Cow</td>
<td>91</td>
</tr>
<tr>
<td>Starvout</td>
<td>179</td>
</tr>
<tr>
<td>Days</td>
<td>333</td>
</tr>
<tr>
<td>Humbug</td>
<td>825</td>
</tr>
<tr>
<td>Happy Camp</td>
<td>165</td>
</tr>
<tr>
<td>Agness</td>
<td>415</td>
</tr>
<tr>
<td>Wsichuck</td>
<td>1,050</td>
</tr>
<tr>
<td>Smith</td>
<td>125</td>
</tr>
</tbody>
</table>

as it neared the Caves population to the southwest. A distinct tonal note in the A-phrase syllables and a tendency for B₃ and B₄ to fuse distinguished this song.

Geographic Extent.—The geographic extent of variants differed (Table 2). The largest exceeded 1,500 km² within the study area, and limited sampling beyond the study area indicates the Days variant exceeded 3,000 km². Five of the variants occupied <5% of the area of the largest.

All variants occupied a fragmented range resulting primarily from natural habitat heterogeneity but also due to human activities (e.g., agriculture, housing, and forest management activities). Groups of males sharing territorial boundaries and surrounded by uninhabited areas seldom exceeded 12–20 singing males, and many included only one to three males.

DISCUSSION

Type I songs of Black-throated Gray Warblers exhibit considerable geographic variation. Several variants were structurally distinct and occupied discrete areas, but others were not, either overlapping other variants geographically or possessing intermediate features between adjacent variants. The most fragmented song populations had high variation even among males within local populations. Some dialects can be identified, but Type I songs of Black-throated Gray Warblers do not exhibit a clear system of dialects in the manner noted among Hermit Warblers (Janes and Ryker 2006) and White-crowned Sparrows (Notebohm 1969, Chilton and Lein 1996).

The high geographic overlap and variability within the region noted in some Type I variants of Black-throated Gray Warblers suggests a dynamic system. New variants appear to arise and spread by gradual infiltration into other song variant areas while other variants decline fracturing into small disjunct song populations, eventually being overwhelmed by more vigorous variants.

Sampling over a 16-year period, representing only five of the song forms reported indicated there was no change in variant boundaries or change in song structure (SWJ and LR, unpubl. data). This evidence suggests that, while this is likely a dynamic system, changes occur over a period of many decades or longer.

The Type I dialects of Hermit Warblers in comparison are more distinct in both structure and geographic distribution (Janes and Ryker 2006), suggesting a long history of independent development. Variation is apparent within dialect areas, but songs with intermediate characteristics between adjacent dialects were rare. Temporal changes in the distribution and structure of dialects appear to occur in a different manner than suggested for Black-throated Gray Warblers. One temporal change has been noted in dialect boundaries of Hermit Warbler dialects in southern Oregon. This involved the advance of one dialect boundary by 6 km and the complementary retreat of the neighboring dialect (SWJ and LR, unpubl. data). A similar system of moving boundaries was described for dialects of White-crowned Sparrows (Chilton and Lein 1996).

The diversity of variants in the region is comparable between Black-throated Gray and Hermit warblers. Nine of the variants of Black-throated Gray Warblers reported occurred in the area where eight dialects of Hermit Warblers song were previously identified (Janes and Ryker 2006). However, Hermit Warblers occupy a much greater portion of the area and exhibit a more continuous distribution. The area occupied by most Black-throated Gray Warbler variants is much smaller due to more limited suitable habitat. The most restricted Hermit Warbler dialect encompassed 688 km². In contrast, five of the eight variants of Black-throated Gray Warblers for which distributions were completely described occurred in areas <250 km².

The considerable variation in Type I song in these two western wood-warblers is in contrast to
the uniformity in first category singing among wood-warblers in eastern North America (Kroodsma et al. 1984, Byers 1996). Western North America, especially southwestern Oregon and northern California, has greater topographic diversity contributing to a fragmented landscape. Geography has an important role in the production and maintenance of song variants. Ridges exceeding 1,000–1,200 m in elevation separated the most distinct song forms.

Fire also has an important role in the age and distribution of the mosaic of plant communities in the region (Agee 1993, Taylor and Skinner 1998), contributing to a fragmented landscape within watersheds. Stand-replacing fires are likely an important factor contributing to periodic isolation of populations and diversity of variants at this finer scale.

ACKNOWLEDGMENTS

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LITERATURE CITED


SEARCH BEHAVIOR OF ARBOREAL INSECTIVOROUS MIGRANTS AT GULF COAST STOPOVER SITES IN SPRING

CHAO-CHIEH CHEN,1,3 WYLIE C. BARROW JR.,2,5 KEITH OUCHLEY,1,4 AND ROBERT B. HAMILTON1

ABSTRACT.—Search behavior of arboreal insectivorous migrants was studied at three stopover sites along the northern coast of the Gulf of Mexico during spring migrations, 1993-1995. We examined if search behavior was affected by phylogeny, or by environmental factors. A sequence of search movements (hop, flutter, or flight) in a foraging bout was recorded for each migrant encountered. Search rate, frequency, and distance of movements were calculated for each species. Search rate was positively correlated with proportion of hop, but negatively correlated to flight distance. Hop distance was positively correlated to tarsus length, as was flight distance to wing length for the 31 species of migrants. Cluster analysis indicated closely related species generally have similar foraging modes, which range from "sit-and-wait" of flycatchers to "widely foraging" of warblers. Migrants tended to use more hops in dense vegetation, but more flights in areas with sparse vegetation. Migrants also used more flights when foraging in mixed-species flocks and during periods of high migrant density. Logistic models indicated warblers were more influenced by environmental factors than vireos, possibly because warblers are near-perch searchers and more affected by these factors.

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Numerous studies have reported on the search behavior of forest birds (Williamson 1971; Morton 1980; Fitzpatrick 1981; Robinson and Holmes 1982, 1984; Holmes and Recher 1986; Hutto 1988; Lovette and Holmes 1995), and some have found that environmental factors affect search behavior of birds. Robinson and Holmes (1982, 1984) in New Hampshire, and Holmes and Recher (1986) in Australia, found that search tactics of insectivorous birds were related to vegetation structure and prey availability. Prey type and distribution and abundance of prey can also affect search behavior of birds (Davies 1977, Griffiths 1980, Graber and Graber 1983, Holmes and Schultz 1988, Lovette and Holmes 1995). Fitzpatrick (1981) concluded that visual field complexity and prey dispersion characteristics are the two most important factors affecting search strategies of tyrant flycatchers.

Many Nearctic-Neotropic migrant species, such as wood-warblers (Parulidae), vireos (Vireonidae), and flycatchers (Tyrannidae), have declined dramatically in the past few decades (Hall 1984; Terborgh 1989, 1992; Peterjohn et al. 1995; Holmes and Sherry 2001; Ballard et al. 2003). Most of these studies have been conducted in breeding (Lynch and Whigham 1984, Wilcove 1985, Robinson 1992, Holmes and Sherry 2001), or wintering areas (Lovejoy 1983, Rappole and Morton 1985, Rappole 1995), and relatively fewer studies have been conducted at stopover sites (Moore et al. 1990, 1995; Rodewald and Brittingham 2002; Butler et al. 2007). Moore (2000) noted the migratory pattern is an important part of the annual cycle, and it is crucial to put more efforts into understanding stopover ecology to complete our knowledge of the Nearctic-Neotropical migration system.

Stopover sites are critical in providing food resources for migrants (Berthold and Terrill 1991, Wang and Moore 1997, Moore 2000). En route migrants are in higher demand of energy at stopover sites compared to breeding areas (Biebach 1996), especially prior to taking off after finishing a long non-stop flight. Most en route migrants search for food intensively and continuously at staging areas (Moore and Wang 1991, this study). We investigated search behavior of arboreal insectivorous migrants at three stopover sites (6 plots) along the northern coast of the Gulf of Mexico in spring, 1993-1995. These stopover sites are within the Chenier Plain, and three of the plots were managed for cattle grazing (Barrow et al. 2000). Our objectives were to examine if search behavior of migrants was affected by: (1) environmental factors (e.g., vegetation structure), (2) social status (flock, high density), or (3) phylogeny.
METHODS

Study Area.—The three study sites were along the northern coast of the Gulf of Mexico: (1) Grand Chenier, Cameron Parish, Louisiana; (2) Hackberry Ridge, Cameron Parish, Louisiana; and (3) Smith Point, Chambers County, Texas. Grand Chenier was a more mature and diverse coastal forest than the other two sites, whereas Hackberry Ridge had a relatively low canopy and consisted predominantly of sugarberry (Celtis laevigata) trees. The Smith Point site had many live oaks (Quercus virginiana) with thick understory vegetation (Barrow et al. 2000).

Each study site consisted of a “disturbed” plot with reduced understory, primarily due to cattle grazing, and a “control” plot where the understory had not been affected. All control plots had significantly more subcanopy and understory vegetation than disturbed plots (Barrow et al. 2000: figure 5). Each plot was to be a 100 X 300-m rectangle, but plots of this size could not be obtained at all sites because of limited availability. Disturbed and control plots were adjacent at Grand Chenier, but separated by 1 km at Hackberry Ridge and by 100 m at Smith Point.

The long axis of each plot was oriented East-West, roughly parallel to the coastline. We established grids marked every 25 m with flags that delineated the boundaries of many small blocks and formed several transect lines within all study plots.

Field Procedures.—Grand Chenier was sampled from 15 April to 15 May 1993. Each site was systematically sampled for a week from 10 March to 17 May 1994 to equalize effort among sites. Five additional days (19-21 Mar, 21-22 Apr) were spent at Smith Point in 1995, because this site had the least data collected from the previous year.

Some species are known to have individuals that overwinter at our sites and they were included in the analysis. These included Yellow-rumped Warbler (Dendroica coronata), Ruby-crowned Kinglet (Regulus calendula), and Blue-headed Vireo (Vireo solitarius), as well as some individuals of Common Yellowthroat (Geothlypis trichas), Blue-gray Gnatcatcher (Polioptila caerulea), and White-eyed Vireo (Vireo griseus).

Foraging behavior of birds in terrestrial habitats has been divided into five basic components: “search,” “attack,” “foraging site,” “food,” and “food handling” (Remsen and Robinson 1990). Search behavior can be further divided into “scanning” and “movement” (O’Brien et al. 1990). “Scanning,” the action of the head and eyes to spot prey, is not included in our study because it is difficult to quantify. We focused on search movements used to locate food or for substrates that contain food. “Search” ends once food or food-hiding substrates are observed and attacked (Remsen and Robinson 1990). Classification of search movements was modified from Remsen and Robinson (1990) as:

“hop”—movements made only with the legs,

“flutter”—movements made mainly with the legs, but with the support of the wings, and

“fly”—movements made by flapping the wings.

In our experience, a bird flies only when the distance between two perches is substantially greater than its body length. Jander (1975) divided flying into two types: flights within patches and flights between patches. A patch could be a tree or a group of connected trees. Flights between patches were used to cross gaps and are for traveling rather than for search. We distinguished between the two types of flights only within-patch flights were included in the analysis.

Search data were recorded as we traversed the study plots. Attempts were made to equalize sampling effort in each part of the plot. We tried not to observe individuals of the same gender of a particular species at the same spot or within a mixed-species foraging flock to avoid collecting data from the same bird. Repeated sampling of individuals should be rare because most Nearctic-Neotropical migrants are known to depart the night of their arrival (Gauthreaux 1971, 1972; Moore and Kerlinger 1987; Kuenzi et al. 1991).

We used “focal sampling” and “continuous recording” following Martin and Bateson (1993). We quietly followed each bird encountered and entered observations into a tape recorder. We recorded species, time of day, presence of migrant fallout (ca. 10-fold increase or greater from previous day), every search movement observed, and the distances the bird moved (in cm: we used the length of the bird to estimate these distances). Only one distance estimate was made for each type of search movement for an individual. We stopped recording once the bird went beyond our view, and sequence and duration information on search movements was later transcribed from the tape.
We noted whether the bird was in a flock or foraging alone. A mixed-species flock is defined as a group of two or more species that move in concert and behave cohesively while foraging (Hutto 1987, 1994). Large numbers of Nearctic-Neotropical migrant landbirds appeared at the study sites from time to time during the study period. These migrant “fallouts” often coincided with occurrence of severe weather conditions, especially thunderstorms (Lowery 1945, 1955; Gaut heap 1971). High migrant density in the plot caused by migrant fallout was also recorded since the density of migrants may increase 10- to 100-fold compared to regular days (Chen 1996; W.C. Barrow, unpubl. data). We recorded whether vine tangles were in the area where the bird had been searching beginning in 1994. Vine tangles were vegetated areas comprised of intertwined vines (most often Vitis spp.) supported by trees, usually sugarberry.

**Statistical Analyses.**—Morrison (1984) recommended that a sample of at least 30 individuals, or about 150 sequential observations, was needed for data analysis of attack behavior or foraging site. We recorded many more search movements than attack behaviors during a foraging sequence. We included species for which we had at least 20 individuals or 200 sequential observations. We excluded search sequences with durations <10 sec. Thirty-one species were included in the analysis (Table 1).

Search rate was defined as the number of search movements per minute (Robinson and Holmes 1982), and was computed by dividing the total number of search movements in a sequence by the sequence duration in minutes. An average search rate was calculated from all sequences for each species. We did not distinguish between within-patch flight and between-patch flight in 1993, and used only data from 1994 and 1995 to calculate flight distance.

The relationships between proportion of hop and search rate, and between flight distance and search rate of the 31 migrants were formulated using a linear model. The two flycatchers were deleted in the former analysis since they primarily used hops to change direction instead of searching for prey. We further examined if hop distance was correlated to tarsus length and whether flight distance was correlated to wing length of migrants. Morphological data were derived from birds banded at the sites (Barrow et al. 2000; Appendix). Search movement, search rate and movement distance were correlated, and we analyzed these three variables together using a cluster analysis. The frequencies of different types of search movement used by a bird, search rate, and movement distance are all related, and we examined these three variables together in a cluster analysis. Cluster analysis with a complete linkage (SAS Institute 1999) was used to group the 31 species by search rate, flight frequency, and hopping distance. Hopping frequency and flight distance were highly correlated to search rate; therefore we used flight frequency and hopping distance in the cluster analysis.

The influence of environmental and social factors, including site, plot, presence of vine tangles, flocking, and migrant density in a plot were examined on search movement of migrants. We used data from 1994 in this part of the analysis because we stayed at only one site in both 1993 and 1995. We pooled all observations of birds in the same family, and found only warblers and vireos had sufficient samples for analysis. A Likelihood-ratio Chi-square test (SAS Institute 1999) was used to evaluate the association between type of search movement and each variable, individually. Logistic models (Agresti 1990, SAS Institute 1999) were used to further test whether these factors collectively affected the frequency of search movements by warblers and vireos. We used a generalized linear model (GLM) to examine if these factors had any effect on search rate and movement distance of warblers and vireos separately (SAS Institute 1999). A Type I error (α level) of 0.05 was chosen for all statistical tests.

**RESULTS**

Search Movements Among Families.—The relative frequencies of hops used by migrants differed among families: warblers 85.0%, vireos 77.0%, tanagers 71.1%, and flycatchers 18.1% (Table 1). The relative frequency of flight was inversely related to frequency of hops for all taxa; flight and hop combined composed a large proportion of search movements. Flycatchers used flight intensively, 82.6% for Acadian Flycatcher (Empidonax virescens) and 81.2% for Eastern Wood-Pewee (Contopus virens). Hooded Warblers (Wilsonia citrina) had the highest relative frequency of flight (22.6%), more than twice that of other warblers. Fluttering was rare (< 5.0%) for most species and flycatchers did not flutter at all (Table 1).
TABLE 1. Sample size, frequency of search movements, and search rate (number of movements/min) of arboreal insectivorous migrants at Gulf Coast stopover sites in spring, 1993–1995.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species code</th>
<th>No. individuals</th>
<th>Hop (%)</th>
<th>Flumer (%)</th>
<th>Fly (%)</th>
<th>Totals</th>
<th>Search rate Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cuculidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-billed Cuckoo (<em>Coccyzus americanus</em>)</td>
<td>YBCU</td>
<td>56</td>
<td>454 (74.4)</td>
<td>31 (5.1)</td>
<td>125 (20.5)</td>
<td>610</td>
<td>6.0 ± 0.6</td>
</tr>
<tr>
<td><strong>Tyrannidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acadian Flycatcher (<em>Empidonax virescens</em>)</td>
<td>ACFL</td>
<td>27</td>
<td>12 (17.4)</td>
<td>0 (0.0)</td>
<td>57 (82.6)</td>
<td>69</td>
<td>1.7 ± 0.3</td>
</tr>
<tr>
<td>Eastern Wood-Pewee (<em>Contopus virens</em>)</td>
<td>EAWP</td>
<td>56</td>
<td>13 (18.8)</td>
<td>0 (0.0)</td>
<td>56 (81.2)</td>
<td>69</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td><strong>Regulidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ruby-crowned Kinglet (<em>Regulus calendula</em>)</td>
<td>RCKI</td>
<td>128</td>
<td>2,378 (82.5)</td>
<td>158 (5.5)</td>
<td>346 (12.0)</td>
<td>2,882</td>
<td>24.7 ± 0.8</td>
</tr>
<tr>
<td><strong>Poliitididae</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Blue-gray Gnatcatcher (<em>Polioptila caerulea</em>)</td>
<td>BGGN</td>
<td>41</td>
<td>869 (85.4)</td>
<td>38 (3.7)</td>
<td>111 (10.9)</td>
<td>1,018</td>
<td>26.6 ± 1.4</td>
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<tr>
<td><strong>Vireonidae</strong></td>
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</tr>
<tr>
<td>White-eyed Vireo (<em>Vireo griseus</em>)</td>
<td>WEVI</td>
<td>80</td>
<td>1,192 (80.9)</td>
<td>104 (7.1)</td>
<td>177 (12.0)</td>
<td>1,473</td>
<td>17.9 ± 0.8</td>
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<td>Blue-headed Vireo (<em>V. solitarius</em>)</td>
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<td>23</td>
<td>238 (68.6)</td>
<td>23 (6.6)</td>
<td>86 (24.8)</td>
<td>347</td>
<td>11.3 ± 1.1</td>
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<tr>
<td>Yellow-throated Vireo (<em>V. flavifrons</em>)</td>
<td>YTVI</td>
<td>18</td>
<td>331 (81.3)</td>
<td>31 (7.6)</td>
<td>45 (11.1)</td>
<td>407</td>
<td>16.2 ± 1.7</td>
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<tr>
<td>Philadelphia Vireo (<em>V. philadelphicus</em>)</td>
<td>PHVI</td>
<td>28</td>
<td>366 (75.9)</td>
<td>19 (4.0)</td>
<td>97 (20.1)</td>
<td>482</td>
<td>13.5 ± 1.1</td>
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<tr>
<td>Red-eyed Vireo (<em>V. olivaceus</em>)</td>
<td>REVI</td>
<td>291</td>
<td>2,639 (78.0)</td>
<td>255 (7.5)</td>
<td>488 (14.5)</td>
<td>3,382</td>
<td>14.6 ± 0.3</td>
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<tr>
<td><strong>Parulidae</strong></td>
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<td></td>
</tr>
<tr>
<td>Blue-winged Warbler (<em>Vermivora cyanoptera</em>)</td>
<td>BWWA</td>
<td>96</td>
<td>1,228 (81.0)</td>
<td>89 (5.9)</td>
<td>199 (13.1)</td>
<td>1,516</td>
<td>24.6 ± 1.2</td>
</tr>
<tr>
<td>Golden-winged Warbler (<em>V. chrysoptera</em>)</td>
<td>GWWA</td>
<td>31</td>
<td>469 (83.5)</td>
<td>31 (5.5)</td>
<td>62 (11.0)</td>
<td>562</td>
<td>22.9 ± 1.7</td>
</tr>
<tr>
<td>Tennessee Warbler (<em>Oreothlypis peregrina</em>)</td>
<td>TEWA</td>
<td>175</td>
<td>2,029 (86.3)</td>
<td>94 (3.9)</td>
<td>239 (9.8)</td>
<td>2,425</td>
<td>20.2 ± 0.8</td>
</tr>
<tr>
<td>Northern Parula (<em>Parula americana</em>)</td>
<td>NOPA</td>
<td>51</td>
<td>649 (84.6)</td>
<td>34 (4.4)</td>
<td>84 (11.0)</td>
<td>767</td>
<td>21.9 ± 1.4</td>
</tr>
<tr>
<td>Yellow Warbler (<em>Dendroica petechia</em>)</td>
<td>YWAR</td>
<td>50</td>
<td>670 (84.8)</td>
<td>51 (6.5)</td>
<td>69 (8.7)</td>
<td>790</td>
<td>25.9 ± 1.4</td>
</tr>
<tr>
<td>Chestnut-sided Warbler (<em>D. pensylvanica</em>)</td>
<td>CSWA</td>
<td>98</td>
<td>1,877 (88.1)</td>
<td>93 (4.4)</td>
<td>159 (7.5)</td>
<td>2,120</td>
<td>29.9 ± 1.2</td>
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<tr>
<td>Magnolia Warbler (<em>D. magnolia</em>)</td>
<td>MAWA</td>
<td>221</td>
<td>4,225 (88.3)</td>
<td>230 (4.8)</td>
<td>330 (6.9)</td>
<td>4,785</td>
<td>30.9 ± 0.7</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (<em>D. coronata</em>)</td>
<td>MYWA</td>
<td>237</td>
<td>3,774 (81.3)</td>
<td>273 (5.9)</td>
<td>596 (12.8)</td>
<td>4,643</td>
<td>20.5 ± 0.6</td>
</tr>
<tr>
<td>Black-throated Green Warbler (<em>D. virens</em>)</td>
<td>BTNW</td>
<td>75</td>
<td>1,617 (84.9)</td>
<td>116 (6.1)</td>
<td>172 (9.0)</td>
<td>1,905</td>
<td>24.9 ± 1.2</td>
</tr>
<tr>
<td>Blackburnian Warbler (<em>D. fusca</em>)</td>
<td>HLBW</td>
<td>26</td>
<td>680 (87.1)</td>
<td>18 (2.3)</td>
<td>83 (10.6)</td>
<td>781</td>
<td>26.9 ± 2.1</td>
</tr>
<tr>
<td>Bay-breasted Warbler (<em>D. castanea</em>)</td>
<td>BBWA</td>
<td>192</td>
<td>3,856 (88.9)</td>
<td>135 (3.1)</td>
<td>348 (8.0)</td>
<td>4,339</td>
<td>25.9 ± 0.6</td>
</tr>
<tr>
<td>Cerulean Warbler (<em>D. cerulea</em>)</td>
<td>CERW</td>
<td>28</td>
<td>502 (88.2)</td>
<td>27 (4.5)</td>
<td>74 (12.3)</td>
<td>603</td>
<td>24.6 ± 1.2</td>
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<tr>
<td>Black-and-white Warbler (<em>Mniotilta varia</em>)</td>
<td>BAWW</td>
<td>131</td>
<td>3,015 (91.9)</td>
<td>76 (2.3)</td>
<td>191 (5.8)</td>
<td>3,282</td>
<td>32.3 ± 1.0</td>
</tr>
<tr>
<td>American Redstart (<em>Setophaga ruticilla</em>)</td>
<td>AMRE</td>
<td>71</td>
<td>1,254 (84.1)</td>
<td>49 (3.2)</td>
<td>194 (12.7)</td>
<td>1,527</td>
<td>26.0 ± 1.3</td>
</tr>
<tr>
<td>Prothonotary Warbler (<em>Protonotaria citrea</em>)</td>
<td>PROW</td>
<td>59</td>
<td>938 (80.7)</td>
<td>92 (7.9)</td>
<td>132 (11.4)</td>
<td>1,162</td>
<td>18.9 ± 1.0</td>
</tr>
</tbody>
</table>
Search rate varied among families: 24.9 movements/min for warblers, 14.7 for vireos, 5.0 for tanagers, and 1.0 for flycatchers (Table 1). Warblers hopped an average distance of 12 cm, vireos 16 cm, and Yellow-billed Cuckoo (Coccyzus americanus), the largest species in this study, 23 cm (Table 2). The average distance of fluttering was 31 cm for warblers, 39 cm for vireos, and 66 cm for Yellow-billed Cuckoo. The average flight distance was 109 cm for warblers, 110 cm for vireos, 252 cm for Yellow-billed Cuckoo, but 432 cm for flycatchers (Table 2). The distance traveled in a hop was roughly proportional to a bird's size, but flight distance was greatly influenced by the foraging mode used by a bird. For example, flycatchers made significantly longer flights than warblers and vireos. The Hooded Warbler, among warblers, had the longest average flight distance (190 cm); this was partly due to its frequent use of wing-powered maneuvers.

Search Movements Among Species.—Birds that hopped more tended to have a higher search rate ($y = -71.43 + 1.13x; r^2 = 0.77, P < 0.001$; Fig. 1), partly because hopping takes the shortest time to complete. Most warblers had a high proportion of "hops," and often had a higher search rate (Table 1). Search rate of migrants was negatively correlated to flight distance ($y = 58.456e^{-0.020x}; r^2 = 0.86, P < 0.0001$; Fig. 2). Hop distance of 31 migrant species was positively correlated to tarsus length ($y = -3.93 + 0.99x; r^2 = 0.24, P < 0.01$; Fig. 3), as was flight distance to wing length ($y = -5.19 + 0.28x; r^2 = 0.24, P < 0.01$; Fig. 4).

Species were divided into three groups in the dendrogram: warblers, vireos and tanagers, and flycatchers (Fig. 5). Species were grouped mainly according to their phylogeny with a few exceptions. The Hooded Warbler was clustered with vireos instead of warblers. The Blue-headed Vireo was clustered with the Yellow-billed Cuckoo, and, as a group, they were linked with tanagers. A further division roughly separated vireos and tanagers, but the Blue-gray Gnatcatcher and Ruby-crowned Kinglet were grouped with warblers. Two subgroups were identified within warblers: Canada Warbler (Wilsonia canadensis), Black-and-white Warbler (Mniotilta varia), Magnolia Warbler (Dendroica magnolia), and Chestnut-sided Warbler (D. pensylvanica) as one subgroup, and all the other warblers except the Hooded Warbler as the other subgroup. The first
TABLE 2. Distance (cm) of search movements of arboreal insectivorous migrants at Gulf Coast stopover sites in spring, 1993–1995. Data under “Fly” were within patch flights and only recorded in 1994 and 1995. Nomenclature for species codes is in Table 1.

<table>
<thead>
<tr>
<th>Species code</th>
<th>Hop</th>
<th></th>
<th></th>
<th>Fly</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean ± SE</td>
<td>n</td>
<td>Mean ± SE</td>
<td>n</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>YBCU</td>
<td>65</td>
<td>22.7 ± 1.7</td>
<td>24</td>
<td>65.8 ± 6.2</td>
<td>44</td>
<td>251.8 ± 24.7</td>
</tr>
<tr>
<td>ACFL</td>
<td>3</td>
<td>23.3 ± 6.7</td>
<td>0</td>
<td></td>
<td>21</td>
<td>341.0 ± 76.4</td>
</tr>
<tr>
<td>EAWP</td>
<td>4</td>
<td>10.5 ± 5.1</td>
<td>0</td>
<td></td>
<td>22</td>
<td>523.6 ± 100.1</td>
</tr>
<tr>
<td>RCKI</td>
<td>83</td>
<td>12.3 ± 9.0</td>
<td>65</td>
<td>25.7 ± 1.5</td>
<td>67</td>
<td>972 ± 9.6</td>
</tr>
<tr>
<td>BGGN</td>
<td>27</td>
<td>16.8 ± 4.2</td>
<td>17</td>
<td>23.8 ± 2.9</td>
<td>27</td>
<td>843.3 ± 8.6</td>
</tr>
<tr>
<td>WEVI</td>
<td>46</td>
<td>15.5 ± 2.0</td>
<td>36</td>
<td>39.7 ± 3.6</td>
<td>33</td>
<td>1152 ± 15.5</td>
</tr>
<tr>
<td>BHVI</td>
<td>8</td>
<td>20.6 ± 4.2</td>
<td>5</td>
<td>42.0 ± 5.8</td>
<td>12</td>
<td>967 ± 16.7</td>
</tr>
<tr>
<td>YTVI</td>
<td>19</td>
<td>17.3 ± 2.8</td>
<td>8</td>
<td>38.8 ± 4.8</td>
<td>10</td>
<td>1060 ± 13.5</td>
</tr>
<tr>
<td>PHVI</td>
<td>25</td>
<td>11.5 ± 1.4</td>
<td>11</td>
<td>35.5 ± 5.3</td>
<td>26</td>
<td>1135 ± 20.7</td>
</tr>
<tr>
<td>REVI</td>
<td>156</td>
<td>13.2 ± 0.8</td>
<td>110</td>
<td>38.2 ± 1.6</td>
<td>76</td>
<td>1213 ± 10.6</td>
</tr>
<tr>
<td>BWVA</td>
<td>40</td>
<td>11.4 ± 1.1</td>
<td>26</td>
<td>31.0 ± 1.8</td>
<td>21</td>
<td>810.1 ± 7.7</td>
</tr>
<tr>
<td>GWWA</td>
<td>15</td>
<td>8.0 ± 1.1</td>
<td>14</td>
<td>33.6 ± 3.6</td>
<td>9</td>
<td>800.0 ± 8.8</td>
</tr>
<tr>
<td>TEWA</td>
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<td>9.3 ± 0.8</td>
<td>39</td>
<td>29.1 ± 1.8</td>
<td>45</td>
<td>918.3 ± 5.6</td>
</tr>
<tr>
<td>NOPA</td>
<td>25</td>
<td>10.4 ± 1.6</td>
<td>10</td>
<td>22.5 ± 4.0</td>
<td>30</td>
<td>920.0 ± 13.7</td>
</tr>
<tr>
<td>YWAR</td>
<td>21</td>
<td>11.4 ± 1.8</td>
<td>20</td>
<td>36.5 ± 2.7</td>
<td>12</td>
<td>725.1 ± 5.8</td>
</tr>
<tr>
<td>CSWA</td>
<td>63</td>
<td>13.1 ± 1.2</td>
<td>40</td>
<td>32.0 ± 2.8</td>
<td>26</td>
<td>1119 ± 18.7</td>
</tr>
<tr>
<td>MAWA</td>
<td>126</td>
<td>12.7 ± 1.4</td>
<td>90</td>
<td>29.1 ± 1.2</td>
<td>71</td>
<td>842.3 ± 11.4</td>
</tr>
<tr>
<td>MYWA</td>
<td>140</td>
<td>9.5 ± 0.6</td>
<td>101</td>
<td>28.9 ± 1.3</td>
<td>170</td>
<td>1289.5 ± 7.7</td>
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<tr>
<td>BTNW</td>
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<td>41</td>
<td>28.4 ± 2.2</td>
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<td>80.0 ± 5.2</td>
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<tr>
<td>BLBW</td>
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<td>12.0 ± 1.8</td>
<td>7</td>
<td>25.7 ± 3.2</td>
<td>29</td>
<td>741.9 ± 9.4</td>
</tr>
<tr>
<td>BBWA</td>
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<td>71</td>
<td>35.5 ± 4.1</td>
<td>102</td>
<td>983.7 ± 7.7</td>
</tr>
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<td>11.2 ± 1.3</td>
<td>7</td>
<td>31.4 ± 0.4</td>
<td>11</td>
<td>152.7 ± 40.4</td>
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<tr>
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<td>11.2 ± 2.4</td>
<td>41</td>
<td>31.7 ± 2.4</td>
<td>43</td>
<td>122.6 ± 22.4</td>
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<tr>
<td>AMRE</td>
<td>45</td>
<td>12.8 ± 1.3</td>
<td>20</td>
<td>35.5 ± 2.9</td>
<td>38</td>
<td>106.6 ± 18.7</td>
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<tr>
<td>PROW</td>
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<td>12.0 ± 2.6</td>
<td>22</td>
<td>29.5 ± 3.2</td>
<td>15</td>
<td>113.3 ± 13.5</td>
</tr>
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<td>10.9 ± 1.3</td>
<td>24</td>
<td>40.0 ± 3.6</td>
<td>23</td>
<td>129.6 ± 25.0</td>
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<tr>
<td>HOVA</td>
<td>30</td>
<td>17.1 ± 3.4</td>
<td>12</td>
<td>28.3 ± 4.4</td>
<td>7</td>
<td>165.7 ± 60.9</td>
</tr>
<tr>
<td>CAWA</td>
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<td>16.2 ± 2.0</td>
<td>17</td>
<td>36.2 ± 3.3</td>
<td>51</td>
<td>190.0 ± 19.0</td>
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<tr>
<td>SUTA</td>
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<td>8.7 ± 1.2</td>
<td>3</td>
<td>26.7 ± 3.3</td>
<td>11</td>
<td>95.5 ± 23.4</td>
</tr>
<tr>
<td>SCTA</td>
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<td>32.5 ± 17.5</td>
<td>9</td>
<td>344.4 ± 88.4</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>12.0 ± 2.0</td>
<td>7</td>
<td>57.1 ± 9.2</td>
<td>20</td>
<td>161.0 ± 22.2</td>
</tr>
</tbody>
</table>

Factors Affecting Search Movements of Warblers and Vireos.—Warblers used different frequencies of search movements among sites, between plots, presence and absence of vine tangles, and high and low migrant density ($P < 0.001$, Table 3). Vireos used different frequencies of search movements between presence and absence of vine tangles ($P < 0.05$, Table 3), and between foraging solitarily and foraging in flocks ($P < 0.001$).

Four logistic models were built due to different amounts of missing data for each variable. The best fitted models contained some higher order interactions for warblers, whereas two-factor interactions appeared to be sufficient for vireos (Table 4). The model indicated that environmental and social factors influenced frequencies of search movements of warblers more strongly than those of vireos. In particular, warblers that foraged in areas with vine tangles and in the control plot of Hackberry Ridge tended to use more hops than flights. Warblers took more hops when searching solitarily during periods of low migrant density, especially at Smith Point. In contrast, warblers used more flights when foraging in mixed flocks, in areas without vine tangles, in the disturbed plots, especially at Grand Chenier. More hops were used by vireos while foraging solitarily at Smith Point, and more flights were used in flocks at Grand Chenier. The generalized subgroup was characterized by high search rates (Table 1).
linear models did not show any significant effect of environmental and social factors or their interactions on search rates and movement distances for warblers and vireos.

DISCUSSION

Search Movements of Migrants.—Suites of intercorrelated foraging characteristics are called foraging modes (Eckhardt 1979, Huey and Pianka 1981), and search movements and associated prey-attack maneuvers are considered important parts of foraging mode (Remsen and Robinson 1990). Species that hop frequently between perches tend to use near-perch maneuvers, whereas species that fly between perches mostly sally for prey (Remsen and Robinson 1990). The ordination of migrants in the dendrogram (Fig. 5) indicates that closely related species had similar foraging modes with “widely foraging” warblers at the top and “sit-and-wait” flycatchers at the bottom. The grouping of species in the dendrogram corresponds largely to their phylogenetic relationships. Movement distances were in proportion to morphological measurements, and search behavior of these en route migrants is, in part, constrained by body size and wing length.

FIG. 1. Search rate of arboreal insectivorous migrants (n = 29 species) was positively correlated to proportion of hop in search movements at Gulf Coast stopover sites in spring, 1993-1995. We excluded the Acadian Flycatcher and the Eastern Wood-Pewee in this analysis as they primarily used hops to change direction instead of searching for prey.

\[ y = 71.43 + 1.13x \]
\[ r^2 = 0.77, P < 0.001 \]

FIG. 2. Search rate of arboreal insectivorous migrants (n = 31 species) was negatively correlated to flight distance at Gulf Coast stopover sites in spring, 1993-1995.

\[ y = 58.456e^{\frac{0.0029x}{}} \]
\[ r^2 = 0.86, P < 0.0001 \]
Three types of foraging modes were identified based on Remsen and Robinson (1990: table 2). First, both Eastern Wood-Pewee and Acadian Flycatcher display a “passive search” strategy. Both species use open perches, sit and wait for prey, take long flights, and catch prey with a long sally. Second, Summer Tanager \( (Piranga rubra) \), Scarlet Tanager \( (P. olivacea) \), Yellow-billed Cuckoo, and possibly Blue-headed Vireos use a “medium-distance search mode.” They use medium to long distance flights, bouts of hopping, sallies and near-perch gleans to attack prey (Chen 1996). The other species, mostly warblers, adopt a "near-surface search mode" and mainly use hops, short flights, and near-perch maneuvers to catch prey. Remsen and Robinson (1990) separated species that flush-chase prey, such as Hooded Warbler and American Redstart \( (Setophaga ruticilla) \), into another foraging mode. We did not find any difference in search behavior between these two species and other near-surface searchers and, except for their conspicuous wing and tail flicking, Hooded Warblers have a search mode closer to vireos than to other warbler species.

O’Brien et al. (1990) proposed that all search behavior could be placed on a “stop-and-go"
FIG. 5. Dendrogram of cluster analysis of 31 arboreal insectivorous migrant species based on search rate, frequency of flight, and hop distance at Gulf Coast stopover sites in spring, 1993–1995. Phylogenetically related species are clustered in the same group. Nomenclature for bird species codes is in Table 1.

continuum from "widely foraging" to "sit-and-wait." The Yellow-billed Cuckoo serves as a good example to illustrate a combination of the two extremes. Yellow-billed Cuckoos mainly forage on large caterpillars (C.-C. Chen, pers. obs.). They usually scan the surrounding area from their perches, occasionally for several minutes. This strategy becomes efficient when prey moves frequently. Their scanning radius was probably large because cuckoos have been observed using "sally-pounce" or taking several quick hops to catch prey at distances >1 m (C.-C. Chen, pers. obs.). Thus, it was efficient to detect large caterpillars from a stationary position. However, due to the relatively low abundance of large caterpillars, cuckoos must move to a new foraging patch from time to time to find another prey. Consequently, the search strategy of Yellow-billed Cuckoos was characterized by a high frequency of flights, long movements, and low search rates; a combination of "sit-and-wait" and "widely foraging."

Factors Affecting Search Movements.—Vegetation structure accounts for a set of opportunities and constraints that influence how a bird moves during foraging (Robinson and Holmes 1982,
TABLE 3. Frequency of search movements of warblers and vireos partitioned by different environmental and social factors at Gulf Coast stopover sites, 1994.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Warblers</th>
<th>Vireos</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hop</td>
<td>Flutter</td>
</tr>
<tr>
<td>Site</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grand Chenier</td>
<td>4,880</td>
<td>216</td>
</tr>
<tr>
<td>Hackberry Ridge</td>
<td>11,079</td>
<td>403</td>
</tr>
<tr>
<td>Smith Point</td>
<td>6,300</td>
<td>205</td>
</tr>
<tr>
<td>Plot</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>10,654</td>
<td>333</td>
</tr>
<tr>
<td>Disturbed</td>
<td>11,605</td>
<td>491</td>
</tr>
<tr>
<td>Presence of vines</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>14,665</td>
<td>587</td>
</tr>
<tr>
<td>Yes</td>
<td>3,901</td>
<td>107</td>
</tr>
<tr>
<td>Flocking</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In mixed flocks</td>
<td>9,147</td>
<td>405</td>
</tr>
<tr>
<td>Solitary</td>
<td>2,745</td>
<td>124</td>
</tr>
<tr>
<td>Migrant density</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>9,732</td>
<td>273</td>
</tr>
<tr>
<td>Low</td>
<td>12,527</td>
<td>551</td>
</tr>
</tbody>
</table>

1984; Holmes and Recher 1986; Barrow 1990). The distance between potential perches is shorter in dense vegetation; consequently migrants hop more in areas with vine tangles than in areas without vines. Dense vegetation also decreases a bird's scanning diameter, and makes it difficult for a bird to search for prey (Fitzpatrick 1981). Thus, hops are preferred to flights for a thorough search in areas with dense vegetation.

Migrants tended to use more "hops" in control plots and at Smith Point and Hackberry Ridge, but used more "flights" in disturbed plots and at Grand Chenier. These results are in accordance with the vegetation of our study plots as control plots were selected to have denser vegetation than disturbed plots. Vegetation was densest at Smith Point (Barrow et al. 2000: figure 5), whereas Hackberry Ridge had a much denser understory than Grand Chenier. The Grand Chenier site had the highest canopy and contained more mature trees than the other two sites. These results are also consistent with other studies. For example, Robinson and Holmes (1984) found that American Redstarts and Red-eyed Vireos (Vireo olivaceus) took more flights in white ash (Fraxinus americana) than other tree species because white ash had lower vegetation density and more evenly distributed leaves than other trees.

Social status such as foraging in mixed flocks and periods of high migrant density also affected search behavior. Both situations involved concentration of many individuals in a relatively restricted area, and consequently the vegetation was densest at Smith Point.
area. The number of birds may increase 10- to 100-fold in these situations. Consequently, space for each individual to search for food was reduced sharply and an increase in social interaction was expected (Morse 1970). Migrants moved quickly when foraging in mixed-species foraging flocks, and used more "flights" than those that foraged solitarily. Morse (1970) found that birds reduce their foraging space in proportion to flock size. Moreover, birds in mixed flocks have to make continual adjustments to match the overall rate of flock progression (Hutto 1988). Thus, migrants in flocks would take more flights to keep pace with other individuals. During periods of fallout, migrants were everywhere in the plots and it appears to be better for a bird to move away from other individuals to reduce conflicts (Moore and Wang 1991). Migrants moved around frequently and more flights were made during periods of high migrant density than during periods of low migrant density.

Holmes and Robinson (1981) indicated vegetation structure strongly affects foraging behavior of perch-gleaners, but had little influence on species that sally to catch prey. In general, the more a particular type of habitat is used by a bird, the greater the bird is affected by that habitat. Most warblers are typical, near-surface searchers, whereas vireos exhibit some medium-distance search. Thus, warblers are more severely affected by environmental factors than vireos. These differences are apparent with the models that contained three-factor interactions for warblers, but had far less high-order interactions for vireos.

En route migrants often move among different habitats at stopover sites (Hutto 1985; Moore et al. 1995; Barrow et al. 2000), and lean birds usually have a higher search rate, more plastic foraging behavior, and use more types of habitat than fat birds (Loria and Moore 1990; Wang and Moore 2005). All transient warblers in our study, except Hooded Warbler and Prothonotary Warbler (Protonatua citrea), had a higher search rate than wintering Yellow-rumped Warblers.

Migrants often have high energy demands at stopover sites. Martin and Karr (1990) also found that migrants increase use of energetically-expensive maneuvers during early spring and late fall migration when insects are limited. Our results indicate that morphology, phylogeny, vegetation structure, and social status also affect search behavior, and thus have a role in shaping exploitation strategies of migrants at stopover sites. Thus, suitable habitat at stopover sites should be identified and managed for migrants to increase their success during migration.

ACKNOWLEDGMENTS

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<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Tarsus (mm) Mean ± SD</th>
<th>n</th>
<th>Wing (mm) Mean ± SD</th>
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</thead>
<tbody>
<tr>
<td>Yellow-billed Cuckoo</td>
<td>50</td>
<td>24.9 ± 3.0</td>
<td>56</td>
<td>143.8 ± 4.6</td>
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<tr>
<td>Acadian Flycatcher</td>
<td>116</td>
<td>15.8 ± 1.7</td>
<td>138</td>
<td>71.3 ± 4.1</td>
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<tr>
<td>Eastern Wood-Pewee</td>
<td>130</td>
<td>13.8 ± 1.0</td>
<td>149</td>
<td>83.1 ± 3.1</td>
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<td>Ruby-crowned Kinglet</td>
<td>55</td>
<td>17.2 ± 3.4</td>
<td>63</td>
<td>56.4 ± 2.6</td>
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<td>Blue-gray Gnatcatcher</td>
<td>35</td>
<td>16.5 ± 2.4</td>
<td>41</td>
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<td>White-eyed Vireo</td>
<td>274</td>
<td>18.6 ± 3.2</td>
<td>300</td>
<td>59.7 ± 3.7</td>
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<tr>
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<td>20</td>
<td>18.0 ± 4.1</td>
<td>29</td>
<td>74.0 ± 1.8</td>
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<td>16.9 ± 4.0</td>
<td>42</td>
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<td>Philadelphia Vireo</td>
<td>28</td>
<td>16.7 ± 1.3</td>
<td>29</td>
<td>65.4 ± 2.1</td>
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<tr>
<td>Red-eyed Vireo</td>
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<td>15.3 ± 3.0</td>
<td>856</td>
<td>78.1 ± 2.5</td>
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<td>Blue-winged Warbler</td>
<td>47</td>
<td>16.7 ± 1.4</td>
<td>56</td>
<td>51.8 ± 2.7</td>
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<td>Golden-winged Warbler</td>
<td>13</td>
<td>16.8 ± 1.4</td>
<td>16</td>
<td>59.7 ± 2.1</td>
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<tr>
<td>Tennessee Warbler</td>
<td>292</td>
<td>16.6 ± 1.6</td>
<td>296</td>
<td>62.2 ± 2.3</td>
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<tr>
<td>Northern Parula</td>
<td>57</td>
<td>16.4 ± 2.0</td>
<td>62</td>
<td>54.9 ± 2.6</td>
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<tr>
<td>Yellow Warbler</td>
<td>30</td>
<td>15.6 ± 3.5</td>
<td>32</td>
<td>61.1 ± 3.0</td>
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<td>Chestnut-sided Warbler</td>
<td>71</td>
<td>16.0 ± 3.2</td>
<td>75</td>
<td>61.7 ± 2.6</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
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<td>16.3 ± 3.1</td>
<td>265</td>
<td>58.6 ± 2.4</td>
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<td>Yellow-rumped Warbler</td>
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<td>1,395</td>
<td>71.8 ± 2.7</td>
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<td>Black-throated Green Warbler</td>
<td>21</td>
<td>16.7 ± 2.9</td>
<td>21</td>
<td>61.1 ± 2.2</td>
</tr>
<tr>
<td>Blackburnian Warbler</td>
<td>17</td>
<td>16.1 ± 2.6</td>
<td>17</td>
<td>67.4 ± 1.8</td>
</tr>
<tr>
<td>Bay-breasted Warbler</td>
<td>152</td>
<td>15.9 ± 3.4</td>
<td>172</td>
<td>72.4 ± 2.7</td>
</tr>
<tr>
<td>Cerulean Warbler</td>
<td>13</td>
<td>16.6 ± 1.6</td>
<td>15</td>
<td>63.5 ± 2.0</td>
</tr>
<tr>
<td>Black-and-white Warbler</td>
<td>292</td>
<td>16.7 ± 2.2</td>
<td>315</td>
<td>67.9 ± 2.7</td>
</tr>
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<td>American Redstart</td>
<td>80</td>
<td>16.8 ± 1.6</td>
<td>88</td>
<td>61.0 ± 2.2</td>
</tr>
<tr>
<td>Prothonotary Warbler</td>
<td>132</td>
<td>16.5 ± 3.5</td>
<td>155</td>
<td>68.2 ± 3.0</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>149</td>
<td>16.3 ± 3.7</td>
<td>185</td>
<td>68.1 ± 2.6</td>
</tr>
<tr>
<td>Common Yellowthroat</td>
<td>106</td>
<td>20.2 ± 2.1</td>
<td>134</td>
<td>54.2 ± 2.9</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>392</td>
<td>19.4 ± 2.7</td>
<td>468</td>
<td>64.1 ± 2.7</td>
</tr>
<tr>
<td>Canada Warbler</td>
<td>41</td>
<td>17.9 ± 3.8</td>
<td>43</td>
<td>64.5 ± 1.7</td>
</tr>
<tr>
<td>Summer Tanager</td>
<td>228</td>
<td>18.6 ± 4.0</td>
<td>302</td>
<td>91.2 ± 3.8</td>
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<tr>
<td>Scarlet Tanager</td>
<td>132</td>
<td>18.3 ± 3.3</td>
<td>188</td>
<td>92.1 ± 3.5</td>
</tr>
</tbody>
</table>
NON-BREEDING ECOLOGY OF LOGGERHEAD SHRIKES IN KENTUCKY

ERIN O'BRIEN1 AND GARY RITCHISON1,2

ABSTRACT.—Populations of Loggerhead Shrikes (Lanius ludovicianus) across North America have been declining, and factors responsible for this decline remain unclear. Few studies have focused on the availability and use of wintering habitat. Our objectives were to ascertain the size and characteristics of Loggerhead Shrike territories, and examine the hunting behavior of shrikes during the non-breeding season. We observed 1,372 hunting attempts by 19 shrikes: arthropods (65.3%) and other invertebrates (23.3%) were the most common prey. Characteristics of habitat at used and randomly selected, apparently unused isolated and continuous perch sites differed ($P = 0.023$ and $P = 0.021$, respectively). Used perches had less grass cover, more bare ground, and denser, shorter vegetation. We found no difference between characteristics of occupied and unoccupied areas ($P = 0.34$). Non-breeding territories in our study were larger (mean = 85 ha) than those reported for shrikes during the breeding season. The availability of suitable winter habitat does not appear to be limiting Loggerhead Shrike populations in Kentucky. However, most Loggerhead Shrikes winter south of Kentucky where densities are higher, and it is possible that availability of suitable habitat might be a limiting factor in some areas.

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Populations of Loggerhead Shrikes (Lanius ludovicianus) have been declining over much of North America for the past several decades (Sauer et al. 2008). Factors potentially contributing to declines in populations of Loggerhead Shrikes include low reproductive success, habitat loss and degradation, and reduced over-winter survival. However, previous studies have revealed no evidence that declines in shrike populations are due to low reproductive success (Esely and Bollinger 2001, Yosef 2001). The availability of suitable shrike breeding habitat is apparently not a limiting factor, at least in some locations (Brooks and Temple 1990, Prescott and Collister 1993, Fomes 2004).

A possible factor in the decline of shrike populations is availability of suitable habitat during the non-breeding season. Gawlik and Bildstein (1993) examined seasonal habitat use and abundance of Loggerhead Shrikes in South Carolina and found no difference in habitat use between breeding and non-breeding seasons. They did not, however, compare the characteristics of occupied and unoccupied areas during the non-breeding season, and were unable to draw conclusions concerning the abundance or suitability of non-breeding habitat. Prey availability may also decline during the non-breeding season, particularly in the northern portion of their wintering range, and characteristics of territories occupied by Loggerhead Shrikes during the non-breeding season may differ from those occupied during the breeding season. For example, shrikes may defend larger territories in response to reduced prey availability during the winter. Previous work involving manipulation of prey availability suggests Loggerhead Shrikes increase territory size or perhaps even abandon territories when prey availability is reduced (Yosef and Deyrup 1998).

The objectives of our study were to: (1) ascertain the size and characteristics of Loggerhead Shrike territories in central Kentucky during the non-breeding season, (2) compare the characteristics of territories used by shrikes during the non-breeding season to those of areas not used by shrikes, and (3) examine the hunting behavior of Loggerhead Shrikes during the non-breeding season.

METHODS

Field Procedures.—We studied shrikes from 1 January to 31 March 2005 and 1 November 2005 to 31 March 2006 in Garrard and Madison counties, Kentucky. Shrikes were located by surveying areas where they had been previously reported (Olson 2006, Peterson 2006) and searching areas of apparently suitable shrike habitat.

We captured shrikes using modified bal-chatri traps (Clark 1968), and banded each with a USGS aluminum band and a unique combination of two or three colored plastic bands. Eight shrikes were also fitted with a tail-mounted transmitter (1.2 g: Model BD-2; Holohil Systems Ltd., Carp, ON, Canada); transmitters were attached to three or...
four centrally located rectrices using dental floss. Radio-marked shrikes were tracked using a receiver (Model TR-4; Telonics Inc., Mesa, AZ, USA) and a 2-element Yagi antenna (Talonics Inc., Mesa, AZ, USA).

We observed the hunting behavior of shrikes from 1 January to 31 March 2005 and 1 November 2005 to 31 March 2006 with all observations between 0800 to 1600 hrs. We recorded perch type (e.g., tree or utility wire), perch height (estimated using previously measured heights, e.g., height of fence posts), time spent on perches, whether the shrike attacked or gave up (flew from perch without initiating an attack) and, for attacks, the outcome (successful, unsuccessful, or unknown) for each hunting attempt. We attempted to identify prey to the lowest taxonomic level possible for successful attacks.

All shrike locations were marked on aerial photographs (Kentucky Office of Geographic Information 2004) to generate territory maps. We obtained fewer locations of shrikes without transmitters and, therefore, all analyses of territory size and composition were based on data from radio-marked shrikes. The six most frequently used hunting perches ($n = 3$ continuous and 3 isolated) were selected in each territory and their characteristics were compared to six randomly selected, apparently unused perches. Random perches were selected by placing a numbered grid over each territory, using a random numbers table to select six grids, then, at the center of those grids, selecting the nearest apparently suitable perch.

Hunting perches were categorized as either continuous (utility wires, fencerows, woodlot edges, and tree-lines; $\geq 20$ m in length) or isolated (isolated trees, shrubs, and snags). Continuous perches were analyzed by placing four 20-m transects parallel to the perch. Each transect was separated by a distance equal to one-half of the perch height (e.g., for a 2-m tall fenceline, the first transect was 1 m from the fence and all transects were 1 m apart) and, along each transect, we sampled vegetation at 5-m intervals. Isolated perches were characterized using four transects radiating from the perch at angles of 36, 72, 108, and 144° (i.e., a 90° area in the direction the shrike most often faced). Transect lengths and distances between sample points ($n = 5$) were based on perch height (i.e., one-half perch height). For example, if an isolated perch was 4 m tall, sample points were at 2-m intervals beginning 2 m from the perch (total transect length = 10 m). Transect directions relative to a perch were based on the direction a shrike most often faced when hunting. A direction was chosen randomly, if there was no directional preference, using a random-numbers table to select a starting point (i.e., isolated perch) or flipping a coin (i.e., continuous perch).

Characteristics of vegetation were described following James and Shugart (1970). We measured litter depth, vegetation height, foliage cover, and type of ground cover (bare ground, grass, herbs, or litter) at each point. Foliage cover was recorded by counting the number of hits (stems or leaves within 1 cm of a 1.5-m pole) at intervals of $0.5$, $0.5-1$, and $1-1.5$ m. A densitometer was used to quantify ground cover.

Habitats in territories of radio-marked shrikes ($n = 7$) were categorized as hayfield ($\geq 95\%$ grasses or herbaceous plants), pasture ($\geq 95\%$ grasses or herbaceous plants and grazed by cattle), old field ($\geq 5\%$ and $\leq 50\%$ woody vegetation with the rest grasses and herbaceous plants), woodlot (wooded area at least 3 trees wide by 3 trees long with tree spacing $\leq 6$ m), and crop field (corn or tobacco). The number of potential perch sites and impaling sites in territories was ascertained by counting the number of shrubs and saplings (woody plants $\geq 1$ m and $\leq 4$ m in height) and trees (woody plants $>4$ m in height), and by measuring the total length of utility wires, fence rows, and tree-lines (row of trees and shrubs with a canopy $\leq 5$ m wide) or woodlot edges (wooded area with canopy $\geq 5$ m wide).

Territory ($n = 7$) boundaries were delineated using the locations of hunting perches plotted on aerial photographs (Kentucky Office of Geographic Information 2004). We constructed polygons by connecting the outer-most points and areas were estimated using Terrain Navigator Pro 7.0 Kentucky (Maptech Software, Billings, MT, USA). Territory characteristics were compared to those in randomly selected, apparently unused areas. Seven unused areas ($n = 3$ in Madison County and 4 in Garrard County) each encompassing 85 ha (the mean size of territories in our study) were randomly selected. Unoccupied areas were selected using aerial photographs (Kentucky Office of Geographic Information 2004). Each image ($46.5$ km$^2$) was assigned a number and selected using a random-numbers table. Areas were further divided into 85-ha squares by
TABLE 1. Mean ± SE perch times, perch heights, and attack distances for hunting attempts where Loggerhead Shrikes in Kentucky attacked or gave up and when shrikes made successful and unsuccessful attacks. Differences are not significant.

<table>
<thead>
<tr>
<th>Attack</th>
<th>Give up</th>
<th>Successful</th>
<th>Unsuccessful</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perch time (min)</td>
<td>2.1 ± 0.1</td>
<td>4.7 ± 0.7</td>
<td>2.6 ± 0.2</td>
<td>2.7 ± 0.4</td>
</tr>
<tr>
<td>Perch height (m)</td>
<td>2.8 ± 0.1</td>
<td>2.9 ± 0.4</td>
<td>3.1 ± 0.2</td>
<td>3.1 ± 0.2</td>
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<tr>
<td>Attack distance (m)</td>
<td>4.3 ± 0.2</td>
<td>3.1 ± 0.2</td>
<td>5.1 ± 0.4</td>
<td>3.4 ± 0.3</td>
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</tbody>
</table>

We found no differences in mean perch time ($F_{1,5} = 0.4, P = 0.58$), attack distance ($F_{1,5} = 0.4, P = 0.54$), or perch height ($F_{1,5} = 3.7, P = 0.11$; Table 1) between successful and unsuccessful attacks. Mean perch time ($F_{1,4} = 0.2, P = 0.66$) and perch height ($F_{1,4} = 5.3, P = 0.08$) did not differ for hunting attempts when shrikes attacked or gave up (Table 1).

Vegetation Analysis.—Characteristics of continuous perches used by Loggerhead Shrikes and those of randomly selected, apparently unused continuous perches differed ($\chi^2 = 0.9, P = 0.021$). Stepwise discriminant analysis revealed that percent grass cover, percent litter cover, foliage cover <0.5 m, and vegetation height permitted the best discrimination between used and unused continuous perches. Continuous perches in areas used by shrikes had less litter and grass cover, more foliage cover <0.5 m, and shorter vegetation (Table 2). Classification analysis using these variables revealed 80% of used and 66.7% of unused sites were correctly classified.

TABLE 2. Mean ± SE characteristics of vegetation associated with continuous perches used ($n = 21$) by Loggerhead Shrikes ($n = 7$) and randomly selected, apparently unused continuous perches ($n = 21$) in Kentucky. Differences are significant ($P = 0.021$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Used</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter depth (cm)</td>
<td>0.76 ± 0.20</td>
<td>0.69 ± 0.33</td>
</tr>
<tr>
<td>Vegetation height (cm)</td>
<td>7.1 ± 0.8</td>
<td>9.7 ± 2.6</td>
</tr>
<tr>
<td>Foliage cover &lt;0.5 m</td>
<td>11.0 ± 1.1</td>
<td>10.0 ± 0.8</td>
</tr>
<tr>
<td>(# of stems)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>58.0 ± 7.1</td>
<td>72.6 ± 6.7</td>
</tr>
<tr>
<td>Herb</td>
<td>9.0 ± 4.5</td>
<td>1.7 ± 0.9</td>
</tr>
<tr>
<td>Litter</td>
<td>5.8 ± 2.9</td>
<td>8.1 ± 4.0</td>
</tr>
<tr>
<td>Bare ground</td>
<td>24.8 ± 4.8</td>
<td>14.3 ± 3.2</td>
</tr>
</tbody>
</table>
TABLE 3. Mean ± SE characteristics of vegetation associated with isolated perches used \((n = 21)\) by Loggerhead Shrikes \((n = 7)\) and randomly selected, apparently unused, isolated perches \((n = 21)\) in Kentucky. Differences are significant \((P = 0.023)\).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Used</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter depth (cm)</td>
<td>1.24 ± 0.18</td>
<td>0.58 ± 0.18</td>
</tr>
<tr>
<td>Vegetation height (cm)</td>
<td>12.7 ± 1.3</td>
<td>11.4 ± 2.3</td>
</tr>
<tr>
<td>Foliage cover &lt;0.5 m (% of stems)</td>
<td>12.6 ± 0.9</td>
<td>10.6 ± 0.8</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>72.2 ± 2.9</td>
<td>71.2 ± 5.0</td>
</tr>
<tr>
<td>Herb</td>
<td>2.7 ± 1.5</td>
<td>9.1 ± 3.3</td>
</tr>
<tr>
<td>Litter</td>
<td>4.7 ± 1.4</td>
<td>6.7 ± 3.3</td>
</tr>
<tr>
<td>Bare ground</td>
<td>17.8 ± 2.5</td>
<td>10.5 ± 3.1</td>
</tr>
</tbody>
</table>

The characteristics of isolated perches used by shrikes and randomly selected, apparently unused isolated perches differed \((\text{Wilks’} \lambda = 0.50, F_{9,32} = 3.3, P = 0.0023)\). Stepwise discriminant analysis revealed that litter depth, percent bare ground, and foliage cover below 0.5 m permitted the best discrimination between used and random isolated perches. Classification analysis correctly categorized 81.0% of randomly selected perches and 77.4% of used perches.

DISCUSSION

Hunting Behavior: Prey Use.—Insects and invertebrates were the most common prey of Loggerhead Shrikes in our study, and only eight vertebrates were taken as prey. Similar results were reported for shrikes during the breeding season in the same area of central Kentucky with arthropods the most common prey \(\text{(Olson 2006, Peterson 2006)}\). Other investigators have also reported insects are typically the most common prey of Loggerhead Shrikes during both the breeding and non-breeding seasons \(\text{(Yosef 1996)}\).

Hunting Behavior: Attacks and Outcomes.—The outcome of hunting attempts by shrikes in our study \(\text{(attacked or gave up and, for attacks, whether successful or unsuccessful)}\) had no effect on mean perch time, perch height, and attack distance. Peterson \(\text{(2006)}\) examined the hunting behavior of Loggerhead Shrikes in the same study area \(\text{(Madison and Garrard counties, Kentucky)}\) during the breeding season and reported similar results. Similar results have been reported for other sit-and-wait predators, including Boreal Owls \(\text{(Aegolius funereus; Bye et al. 1992)}\) and Eastern Screech-Owls \(\text{(Megascops asio; Abbuzzese and Ritchison 1997)}\).

Perch times of Loggerhead Shrikes were similar during the breeding \(\text{(Olson 2006, Peterson 2006)}\) and non-breeding \(\text{(our study)}\) seasons in central Kentucky \(\text{(Table 5)}\). Other investigators have found perch times are more affected by prey selection than season \(\text{(Temeses 1985, Bildstein 1987, Sonerud 1992)}\). The diet of Loggerhead Shrikes in central Kentucky consisted primarily of invertebrates during both breeding and non-
breeding seasons and, as a result, perch times exhibited no seasonal difference.

Mean perch height and attack distances in our study were less than half those reported for Loggerhead Shrikes in the same study area during the breeding season (Olson 2006, Peterson 2006; Table 5). Morrison (1980) compared the hunting behavior of Loggerhead Shrikes during pre-breeding (Dec–Mar) and breeding (Mar–Jul) periods and found perch heights and attack distances increased significantly during the breeding season. Seasonal differences in perch height and attack distance may be due to seasonal differences in vegetation height. Vegetation at perch sites used by shrikes during the non-breeding season in our study was shorter than at perches used during the breeding season in the same study area (Peterson 2006). Shrikes may use higher perches when ground vegetation is taller and denser to provide "a wider view of surrounding vegetation" (Morrison 1980: 297). Increasing perch height in tall vegetation improves prey visibility, especially for detecting prey beneath taller vegetation (Andersson et al. 2009), and also enables predators to detect prey at greater distances (Sonerud 1992, Andersson et al. 2009). The ability to detect prey further from higher perches may explain the longer attack distances of shrikes during the breeding period. Positive relationships between perch height and attack distance have also been reported for other sit-and-wait predators (Sonerud 1980, 1992; Carlson 1985).

**Characteristics of Perch Site Habitat.**—We found perches used by shrikes were generally in areas with shorter, but denser vegetation, and deeper litter compared to randomly selected, apparently unused sites. Other investigators have reported Loggerhead Shrikes often occur in areas with short vegetation (Bohall-Wood 1987, Smith and Kruse 1992, Gawlik and Bildstein 1993). However, areas used by shrikes must also exhibit some structural heterogeneity or patchiness. For example, Michaels and Cully (1998) reported shrikes occurred in areas where vegetation exhibited high structural heterogeneity, i.e., sites with less vegetative cover and more bare ground, but with taller vegetation. Structurally complex habitats with areas of both shorter vegetation and taller (or, as in our study, denser) vegetation may provide habitat for a diverse prey base, including invertebrates and small mammals, while simultaneously enhancing visibility and the ability of shrikes to detect prey.

** Territory Characteristics.**—Mean territory size (85 ha) of Loggerhead Shrikes during the non-breeding season in our study was larger than reported during the breeding season in Kentucky (9 ha; Peterson 2006), Missouri (4.6 ha; Kriebelbaugh 1982), Alberta (8.5 ha; Collister and Wilson 2007), and Florida (8.3–10.1 ha; Yosef and Gruth 1993, 1994). Seasonal differences in range sizes of Loggerhead Shrikes and, specifically, the relatively large winter ranges in our study, may be due to differences in prey availability. Yosef and Deyrup (1998) demonstrated the effect of prey availability on size of Loggerhead Shrike territories by experimentally reducing insect populations in breeding territories; territory size increased by an average of 138% in response to this treatment.

Characteristics of areas used by Loggerhead Shrikes in our study did not differ from those of apparently unused areas, indicating apparently suitable habitat remained unoccupied. Investigators have also reported no differences between characteristics of breeding territories of Loggerhead Shrikes and randomly selected, apparently unused areas (Brooks and Temple 1990, Esely and Bollinger 2001, Fornes 2003, Olson 2006, Peterson 2006). These results suggest that, at least in some areas, Loggerhead Shrike populations are not limited by availability of suitable habitat.

Availability of wintering habitat does not appear to be a limiting factor for Loggerhead Shrikes in central Kentucky, but little is known about the quality and availability of wintering habitat in other parts of their winter range. Further south in their wintering range where densities are higher than in Kentucky (Hobson and Wassenaar 2001, Stedman and Allen 2003, Pérez and Hobson 2007), Loggerhead Shrikes may exhibit intraspecific competition for suitable wintering sites that could influence over-winter survival. For example, Pérez and Hobson (2009) identified resident
and migrant Loggerhead Shrikes wintering in northeastern Mexico using stable isotopes and found residents occupied areas with more bare ground than areas occupied by migrants. If this difference results from competition between residents and migrant shrikes, assuming residents occupy more optimal habitat and bare ground is an important measure of habitat quality, these results suggest availability of optimum habitat may be limited and could affect over-winter survival (Pérez and Hobson 2009).

Mortality.—Two of eight radio-marked shrikes in our study were apparently killed by hawks; other investigators have also noted that shrikes may be vulnerable to hawk predation. For example, Walter (1979) reported that Eleonora’s Falcons (Falco eleonorae) prey on birds migrating across the Mediterranean Sea, and an estimated 15–20% of all birds taken are shrikes (Red-backed Shrikes [L. collurio], Lesser Grey Shrikes [L. minor], and Woodchat Shrikes [L. senator]). Cade (1995) suggested shrikes may be particularly vulnerable to predators because they are not very maneuverable in flight. Their relatively poor flying ability, in combination with conspicuous plumage, may make shrikes attractive targets for predators (Yosef 1994). Vulnerability to hawk predation may be contributing to the decline in shrike populations.

ACKNOWLEDGMENTS

We thank Brian Davidson, Matt Thumayer, Gabe Jenkins, Ryon Dunbar, Nicole Beaver, Emily Clements, Sara Asher, and Carrie Slone for assisting with the fieldwork. C. E. Braun and two anonymous reviewers for helpful reviews of our manuscript, and the Kentucky Department of Fish and Wildlife Resources for financial support.

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Peterson, N. R. 2006. Territory size, habitat use, hunting behavior, and reproductive success of Loggerhead Shrikes in central Kentucky. Thesis. Eastern Kentucky University, Richmond, USA.


SEX AND AGE RATIOS OF BICKNELL’S THRUSH WINTERING IN HISPANIOLA

JASON M. TOWNSEND,†1,4 CHRISTOPHER C. RIMMER,2 ANDREA K. TOWNSEND,1 AND KENT P. MC FARLAND2

ABSTRACT.—We investigated sex and age ratios of wintering Bicknell’s Thrush (Catharus bicknelli) across a geographic gradient of sites on Hispaniola. The island-wide proportion male was 0.64 (n = 127), which is comparable to the known male bias in breeding areas. The proportion male varied geographically on Hispaniola, suggesting some level of habitat segregation. Male-biased ratios occurred at two sites whereas sex ratios at five sites did not differ from parity. The island-wide proportion adult was 0.72 and age ratios were significantly adult-biased at two sites. We assessed vegetative structure at all sites and the proportion of male thrushes increased significantly with density of understory vegetation. Age ratios were not associated with vegetation characteristics. Neither sex nor age ratios varied significantly with elevation. Our data suggest the possibility of sexual habitat segregation with males preferentially occupying cloud forest sites characterized by a thick understory of vines and saplings occurring at densities >10,000 stems/ha.

Received 19 April 2010. Accepted 1 January 2011.

Males and females of many migratory songbirds compete directly for territories and accompanying resources during the non-breeding season. One possible outcome of intersexual competition is habitat segregation, in which disproportionate numbers of either males or females occupy a habitat-type distinct from that occupied predominantly by the other (Lynch et al. 1985). Winter sexual habitat segregation has been confirmed in at least 11 species of Nearctic-neotropical migrants (Ornat and Greenberg 1990, Wunderle 1995, Greenberg et al. 1997, Latta and Faaborg 2001, Marra and Holmes 2001, Latta and Faaborg 2002, Roberts 2007). Age-based habitat segregation, although not as well documented, has been reported for at least two species (Stutchbury 1994, Marra and Holmes 2001).

Habitat segregation by wintering individuals attempting to maximize exclusive access to limited resources may be an important component of overall population regulation (Marra and Holmes 2001, Latta and Faaborg 2002, Runge and Marra 2005). Winter habitat quality can influence survival probability during the non-breeding period and affect fitness during the breeding period (Norris et al. 2004, Reudink et al. 2009). Consequences for individuals relegated to sub-par winter habitat can include loss of body mass over the course of the winter and lower interannual survival (Marra and Holmes 2001). Several studies have indicated that female survival may be particularly limited during the winter period due to competitive exclusion from the highest quality habitats, potentially contributing to male-skewed sex ratios frequently documented for migratory passerines (Benkman 1997, Marra and Holmes 2001, Donald 2007).

Bicknell’s Thrush (Catharus bicknelli), a Nearctic-neotropical migrant of high conservation concern (Wells 2007, Lebbin et al. 2010), is a Red List species considered globally Vulnerable by the International Union for the Conservation of Nature (IUCN) (BirdLife International 2000). The winter range of the species is limited and highly fragmented with most of the population wintering on Hispaniola (Rimmer et al. 2001). The species’ breeding distribution is also highly fragmented, and several breeding populations have disappeared or are known to be declining, leading to listing as a Threatened species in Canada and as a Species of National Concern in the U.S. (Rimmer et al. 2001). Males outnumber females in breeding areas by ~2:1 (Rimmer et al. 2001, Townsend et al. 2009), and it is possible that events in winter areas influence this biased sex ratio (Marra and Holmes 2001). Species that are listed by the IUCN as Vulnerable, Endangered or Critically Endangered (together, “Globally Threatened”) have sex ratios significantly more male-biased than non-threatened species, and the skew becomes greater as populations dwindle.
toward endangered and extinct status (Donald 2007).

The goal of our study was to document the sex ratio of wintering populations of Bicknell’s Thrush for comparison to that of breeding populations. This information could lay the framework for investigating where females are limited, if the winter population is equally male-biased. We classified male:female ratios and age ratios of mist-netted thrushes at seven sites across Hispaniola. We also quantified local vegetation characteristics at each site to evaluate the potential influence of forest structure on sex and age ratios. Our primary objectives were to: (1) document sex and age ratios of Bicknell’s Thrush across an array of sites that spanned most major geographic areas in which the species is known to occur in Hispaniola, (2) describe any deviation in sex and age ratios among these sites and between winter and breeding areas, and (3) characterize and compare the relationship between forest structure and sex and age ratios at each site.

**METHODS**

**Field and Laboratory Procedures.**—We captured Bicknell’s thrushes at seven rain forest and cloud forest sites between January and March 2004 on Hispaniola. (1) Cordillera Central, the largest and highest elevation mountain range in the Dominican Republic with a well-managed system of preserves (Perdomo and Arias 2008). (2) Sierra de Bahoruco, a mountain range in the south-central part of the island that is largely protected as a national park (Townsend et al. 2010). (3) Massif de la Hotte, a mountain range on the southwestern end of Haiti’s Tiburon Peninsula that is tenuously protected as the Pic Macaya Biosphere Reserve (Rimmer et al. 2005). (4) Sierra Martin Garcia, a peninsular mountain range on the southcentral coast of the Dominican Republic that is partially protected as a national park. (5) Sierra de Neiba, a mountain range along the Haiti-Dominican Republic border that has been developed extensively for agriculture. The western high peaks area is formally protected as a national park in the Dominican Republic but illegal settlers and loggers are common (Rimmer et al. 2004, Townsend and Rimmer 2006). (6) Cordillera Septentrional, a mid-elevation mountain range in northcentral Dominican Republic with protected areas managed by cooperative agreements between government and non-governmental agencies (Townsend et al. 2010). (7) Los Haitises, a swath of low-elevation, coastal rainforest in eastern Dominican Republic protected as a national park (Perdomo and Arias 2008).

We captured thrushes in 6- and 12-m mesh mist nets primarily by playback of conspecific vocalizations. We examined rectrices and greater covert tips to classify age of birds (Collier and Wallace 1989). Birds classified as “adults” were >1 year of age, whereas birds classified as “first winter” were born during the previous breeding season. We collected blood from all birds for molecular analysis by puncturing the brachial vein with sterile 27-gauge needles. Blood was harvested in capillary tubes and stored in Queen’s lysis buffer (Seutin et al. 1991). DNA was extracted in the laboratory, using Perfect gDNA Blood Mini kits (Eppendorf) following the manufacturer’s protocol. We amplified homologous sections of sex chromosome-based chromo-helicase-DNA-binding (CHD) genes by polymerase chain reaction (PCR) and viewed the PCR product on an agarose gel to distinguish single CHD-Z male bands from double CHD-Z and CHD-W female bands (Griffiths et al. 1998).

Vegetation structure was characterized for each geographic area where we captured Bicknell’s Thrush using a modified version of the James and Shugart (1970) sampling method for forested habitat. We established five 5-m radius circular plots within each geographic area at random distances and bearings from points of thrush capture. Each circular plot was divided into quadrants along cardinal directions. We counted all trees, shrubs, and herbaceous plants within each quadrant crossing a plane at chest height (~ 1.5 m) in the following categories: shrubs <2 cm diameter at breast height (DBH), small trees 2–10 cm DBH, medium trees 11–20 cm DBH, and large trees >20 cm DBH. Mean measurements at each site were scaled to estimate vegetative cover per hectare in each category and total tree cover basal area.

**Statistical Analyses.**—We used Chi-square ($\chi^2$) goodness of fit (GOF) tests to examine variation in the proportion male and proportion adult. We analyzed the relationship between elevation and proportion male/proportion adult using linear regression. We examined the relationship between proportion male, proportion adult, and forest vegetation characteristics using a generalized linear model (GLM) with mean proportion male or adult in each geographic area as the response variable and the four vegetation categories as the
predictors, weighted by sample size, specifying binomial errors and logit-link function.

RESULTS

The island-wide sex ratio for all sites combined was significantly male-biased (0.64, $\chi^2_1 = 9.7$, $P = 0.002$), but did not differ from the proportion male expected (0.67) based on the sex ratio observed in breeding areas ($\chi^2_1 = 0.6$, $P = 0.45$). The sex ratio varied among geographic areas with two sites male biased (Pueblo Viejo $\chi^2_1 = 6.8$, $P = 0.009$; Cordillera Central $\chi^2_1 = 5.4$, $P = 0.02$) and five sites not varying significantly from 50:50 (Table 1). The number of shrubs/ha in a GLM was a significant predictor of the proportion male ($\chi^2_1 = 4.24$, $P = 0.04$) whereas all other vegetation characteristics showed no significant relationship (small trees: $\chi^2_1 = 0.47$, $P = 0.49$; medium trees: $\chi^2_1 = 1.5$, $P = 0.22$; large trees: $\chi^2_1 = 0.26$, $P = 0.61$). The proportion male at three sites with >10,000 stems/ha was significantly male-biased ($\chi^2_1 = 13.8$, $P < 0.001$), whereas the proportion male did not differ from parity ($\chi^2_1 = 0.9$, $P = 0.35$) at four sites with <8,000 stems/ha (Table 2). There was little variation in non-shrub-layer vegetation characteristics between sites with one notable exception. Total basal area of trees at Los Haitises was 39-56% lower than at other sites, reflecting the historical and on-going deforestation impacts of shifting agriculture on this area (Table 1). Proportion male did not vary significantly with elevation ($F = 0.03$, $P = 0.9$).

The age ratio was significantly adult-biased at two sites (Cordillera Central: 1.0, $\chi^2_1 = 15$, $P < 0.001$; Los Haitises: 0.79, $\chi^2_1 = 8.2$, $P = 0.004$). The proportion adult for all sites combined was 0.73. None of the vegetation classes in a GLM with proportion adult as the response variable had significant predictive value (shrubs: $\chi^2_1 = 2.52$, $P = 0.11$; small trees: $\chi^2_1 = 1.14$, $P = 0.29$; medium trees: $\chi^2_1 = 2.99$, $P = 0.08$; large trees: $\chi^2_1 = 3.05$, $P = 0.08$). Proportion adult did not vary with elevation ($F = 0.3$, $P = 0.6$).

DISCUSSION

Our results indicate the island-wide sex ratio of wintering Bicknell’s Thrush is equivalent to the male-biased sex ratio documented in breeding areas (Townsend et al. 2009). This suggests a year-round male-skewed sex ratio of ~2:1 for Bicknell’s Thrush and raises the question of how this might affect the overall population dynamics.
TABLE 2. The proportion male and proportion adult of wintering Bicknell’s Thrush captured at sites on Hispaniola characterized by differing levels of understory density.

<table>
<thead>
<tr>
<th>Understory density</th>
<th>Total birds captured</th>
<th>Proportion male</th>
<th>Proportion adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;10,000 stems/ha</td>
<td>33</td>
<td>0.76</td>
<td>0.77</td>
</tr>
<tr>
<td>&lt;8,000 stems/ha</td>
<td>74</td>
<td>0.55</td>
<td>0.69</td>
</tr>
</tbody>
</table>

of this species. A review of adult sex ratios in birds found that species listed as Globally Threatened by the IUCN had male-skewed sex ratios in comparison to non-threatened species (Donald 2007). This review offered a series of five non-independent explanations, each of which highlighted conservation implications. Among these was the possibility that intersexual competition during the non-breeding season forces smaller-bodied females to occupy inferior-quality winter habitat (Benkman 1997, Marra and Holmes 2001). Under these circumstances, winter habitat quality could limit female survivorship with implications for overall population dynamics (Marra and Holmes 2001).

Our data suggest that Bicknell’s Thrushes have some sexual habitat segregation on Hispaniola. We currently cannot evaluate the extent to which female thrushes may be limited in wintering areas, but our results suggest that future investigation should pursue this possibility. Our data also indicate that certain areas are preferentially occupied by males and that differential habitat occupancy may be proximately related to characteristics of the forest understory. Males were numerically dominant in high-elevation forests with a thick understory of vines and small trees occurring at densities >10,000 stems/ha. The understory vegetation at other sites, where sex ratios did not differ significantly from parity, was relatively more open occurring at mean densities <8,000 stems per ha. Bicknell’s Thrush compete during the winter for exclusive access to territories (Townsend et al. 2010), and it is possible that understory density is a key component of habitat quality. A radiotelemetry study of wintering Bicknell’s Thrush indicated that individuals in the Sierra de Bahoruco (a male-biased site) were detected most frequently in the densest microhabitats (Townsend et al. 2010). Thrushes wintering at this site primarily consumed arthropods, whereas thrushes at an open understory site in the Cordillera Septentrional (an equal sex-ratio site) mainly consumed fruit (Townsend et al. 2010). It is possible that territory holders in male-dominated habitats derive distinct benefits from dense understory thickets, including protection from predators and a steady, abundant source of arthropods, which may serve as a higher quality winter food source than fruit (Long and Stouffer 2003, Diggs 2008).

The proportion male did not vary significantly with elevation across Hispaniola; however, the two most male-biased sites were in high-elevation cloud forest. It is possible that elevation in isolated areas of Hispaniola provides a buffer against human agricultural disturbance allowing for persistence of intact, dense-understory cloud forest (Latta et al. 2003). The densest patches of understory within this forest type are preferred by Bicknell’s Thrush (Townsend et al. 2010) and are frequently the result of storm-related blowdowns. This suggests the need to better understand the interactions among severe weather dynamics, intact forest that is isolated from human agricultural activity, and quality Bicknell’s Thrush habitat.

The geographic variation in sex ratios of Bicknell’s Thrush across Hispaniola highlights the importance of sampling a broad array of habitats and locations when assessing a species’ winter social structure. We suggest that drawing conclusions about the distribution of males and females from studies at only one or two sites of similar habitat might fail to reveal broader population-level patterns. The sex ratio among American Redstarts (Setophaga ruticilla) in Jamaica, for example, varied from 50:50 at only two of six study sites along a gradient from natural to agricultural habitats (Johnson et al. 2006). Only two of seven geographic areas in our study were strongly male-biased with the remainder having no significant variation from an equal sex ratio. Sex ratios and habitat quality are likely to vary along a wide gradient of available habitats with many permutations of intermediate quality (Latta and Faaborg 2002, Johnson et al. 2006). Intermediate sites are likely to influence fitness and demographics for a large portion of a given species’ population.

The proportion of adults in the population in contrast to sex ratios, had no association with forest structure and little variation among sites. Evidence from our study suggests Bicknell’s Thrush on Hispaniola do not segregate by age class. The evidence also suggests relatively low
recruitment rates for this species with first-winter birds comprising just 28% of the sample. This might be expected in a single-brooded species that nests in a harsh climate with high rates of nest failure (Rimmer et al. 2001).

Our results are preliminary, but they suggest several possibilities and future directions for research. Further studies are needed to examine the fitness consequences for Bicknell’s Thrush wintering in dense understory, male-biased sites versus sites with an open understory, and equal sex ratios. Robust comparisons of habitat quality will require more detailed data on agonistic interactions, the role of body size variation in structuring habitat occupancy, food resource availability, levels of site fidelity, and annual survivorship at a range of overwinter sites. This information could clarify the role of habitat segregation in limiting female survivorship and help inform effective land conservation strategies for this rare, Globally Vulnerable species.

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LITERATURE CITED


RIMMER, C. C., K. P. McFARLAND, W. G. ELLISON, AND J.


ABSTRACT.—Use of ultraviolet (UV) light, which causes porphyrin pigments in feathers of some birds to fluoresce, provides a simple, effective means of distinguishing multiple generations of flight feathers in owls. This permits easier and more accurate classification of age of adult owls. This lighting technique has been used extensively with Barn Owls (Tyto alba) and Northern Saw-whet Owls (Aegolius acadicus) and works well on a variety of owl species at night in the field, and should have wide applicability among owl researchers. The relative ages of the feathers can be easily distinguished by the intensity of fluorescence they exhibit when the ventral surfaces of primaries and secondaries are exposed to UV (black) light. This allows rapid and accurate assessment of molt and, in turn, the assignment of an age classification for the owl. Received 10 August 2009. Accepted 9 January 2011.

Feather molt among owls is complex but occurs in a relatively predictable sequence for an individual species, varying from complete or near-complete annual flight feather replacement in some species to a much lengthier process that may require 3 to 6 years (e.g., Great Horned Owl, Bubo virginianus). The replacement sequence of primaries and secondaries is relatively predictable, and it is believed possible to accurately assign age of individuals of some species to the third, and possibly fourth, year (Pyle 1997). However, distinguishing subtle differences between third- or fourth-generation feathers by looking for contrasts in wear and color can be difficult, especially at night under incandescent light.

Porphyrins are a large group of pigments characterized by nitrogen-containing pyrole rings including chlorophyll and, in animal blood, heme (McGraw 2006). Porphyrins are used by many birds to pigment eggshells in the oviduct, but 13 Orders of birds also use porphyrins as a plumage pigment, most notably owls, goatsnakes, bustards, and turacos (Gill 1995, McGraw 2006). Porphyrins are easily destroyed by exposure to sunlight, and are most abundant in new feathers; many of the so-called natural porphyrins also fluoresce brightly when exposed to ultraviolet (UV) light (Gill 1995). Most natural porphyrins contain iron, but several are based on copper, including turacoverdin, which produces intense green coloration in some turacos, two galliforms, and the jacanas (Dyck 1992); and turacin, responsible for magenta coloration in turacos (Gill 1995). Porphyrins were first isolated from bird feathers in the early 20th century, but their role in feather structure and function, and their synthesis with regards to plumage formation, remain largely unexplored (McGraw 2006).

In this paper, we describe a technique using UV fluorescence of porphyrins to more easily classify age of owls by examining flight feathers and molt patterns.

HISTORY

In 1982, Colvin was studying the interactions of Barn Owls (Tyto alba) and farm rodents by lacing non-toxic rodent baits with tetracycline, which would make rodent bones and teeth (collected from Barn Owl pellets) fluoresce under black UV light. Colvin was also trying to find easier ways to quickly distinguish molt limits among adult Barn Owl flight feathers, especially when working at night under weak incandescent light (e.g., a 6-volt flashlight). He subsequently tried both “white” and long-wave “black” hand-held fluorescent lights, discovering they both made molt patterns easier to see, because newly molted feathers have higher concentrations of porphyrins and fluoresce much more brightly, contrasting with weaker fluorescence in older feathers.

Colvin did not publish his findings and, for many years, the technique was used only by a limited number of researchers who had been...
associated with him or his colleagues in Ohio or New Jersey, working primarily with Barn Owls. In the mid-1990s, Brinker learned of the method from Scott Butterworth, then with the West Virginia Division of Natural Resources, and taught it to Huy, who began using black UV light in October 2000 on Northern Saw-whet Owls (Aegolius acadicus), netted for banding during autumn migration in Maryland. Brinker and Huy alerted Weidensaul, and all three used the technique extensively over the next several years to assign age to adult owls.

This method has since been adopted widely by participants in Project Owlnet, a collaborative network of more than 100 owl migration banding sites, which annually band 8,000 to 15,000 Northern Saw-whet Owls (http://www.projectowlnet.org/). It has proven especially helpful in distinguishing after-second-year/after-third-year (ASY/ATY) adults, which are marked by the presence of three generations of feathers, a frequently subtle distinction that can be difficult to make in the field, at night, under artificial light. The recapture of marked, known-age owls in subsequent years has demonstrated that intensity of UV fluorescence in the flight feathers corresponds to the relative ages of the feathers themselves, and is consistent with accepted, age-linked molt sequences described in Pyle (1997). The importance of this technique lies in the ability it gives even inexperienced workers to quickly and easily distinguish molt limits in owls, and thus facilitate accurate age classification.

**OBSERVATIONS**

Use of UV light to read molt limits has proven successful in a variety of North American owl species. We primarily refer to Northern Saw-whet Owls, but given the assumed universality of porphyrins in owl plumages, this technique should be applicable to most, if not all, tytonids and strigids.

Colvin originally experimented with a variety of “white” fluorescent and long-wave “black” fluorescent lights, but most banders now use commercially available long-wave black UV light bulbs. Good results have been obtained with a 13-watt compact fluorescent blacklight (e.g., Feit Electric BPESL15T/BLB, available from on-line distributors) with a screw-in base for use in lamps taking household incandescent bulbs. There are a variety of handheld battery-powered lights (e.g., Arachnid A49 LED flashlight), powered by AA batteries, that are useful for field applications where 120v AC is not available.

The ventral surfaces of newly molted flight feathers fluoresce an intense magenta color with the UV light positioned ~15 cm away, brightest in the proximal third of the feathers, and fainter or absent from the distal third (Fig. 1). Underwing coverts fluoresce similarly. Porphyrins are generally reddish or brownish pigments, but the fluorescence is often brightest in areas that appear in natural light to be white or lightly tinged with pink.

Most individuals exhibit little fluorescence on dorsal wing surfaces, although it is unclear whether this is the result of rapid degradation of porphyrins in sunlight, or of limited deposition in those areas. Prior to widespread use of UV on the ventral wing surface, molt limits were evaluated using incandescent light to assess the differences in feather wear and sunlight-related fading on the dorsal surface of the feathers. These differences are often subtle and difficult to detect, making accurate assignment of age to owls more prone to error.

There is usually little fluorescence on the rectrices, except where the bases of the feathers are covered by coverts, even though Northern Saw-whet Owls undergo a complete and nearly simultaneous replacement of the tail during the prebasic molt (Collins 1961, Rasmussen et al. 2008). Tarsal and adult ventral down feathers glow with an especially bright, ruby-red color. A hatch-year (HY) Northern Saw-whet Owl, molting from its juvenal “chocolate” plumage in July in coastal Washington, had a mix of fluorescence on its underparts: the brown or fawn juvenal feathers exhibited no color under black UV light, while newly molted feathers glowed brightly (Jamie Acker, Dawn Garcia, and Stan Rullman: pers. comm.). The remiges showed a bright, even fluorescence, while the rectrices had no fluorescence at all. Northern Saw-whet Owl ventral contour feathers show almost no fluorescence in all ages and plumages.

HY Northern Saw-whet Owls captured in fall migration show an even fluorescence across the underwing surfaces, being most intense in the inner primaries and outer secondaries, and fading significantly across the innermost secondaries, which show little or no fluorescence (Fig. 1A). Second-year (SY) owls captured in fall, which have replaced outermost primaries and innermost secondaries (most often primaries 6–10 and...
secondaries 8–12; DFB, unpubl. data), show a distinctive pattern of bright fluorescence in these areas, separated by a block of older retained juvenal feathers with relatively little fluorescence, limited to the base of the flight feathers (Fig. 1B). Owls showing a mix of old and new feathers, but not in the sequential block pattern of a SY (Fig. 1C), are classified as after-second-year (ASY), after Pyle (1997).

Extremely old feathers, presumably those at least 2 years of age, appear chalky or yellowish white under black UV light, evidencing no sign of fluorescence. Distinguishing third-generation feathers from second-generation feathers can be challenging, requiring significant experience on the part of the bander, particularly when working under artificial light at night. However, the difference under UV light is usually easily apparent, even to relatively inexperienced workers. Thus, use of UV light greatly improves the accuracy of age classification of Northern Saw-whet Owls.

FIG. 1. Paired views of ventral surfaces of Northern Saw-whet Owl wings, photographed in October–November under visible light and ultraviolet light. Hatching-year (A) showing even fluorescence across all underwing surfaces; second-year (B) showing contrast between strong fluorescence on newly molted outermost primaries and innermost secondaries; and after-second-year (C) showing three generations of feathers, including chalky-white retained juvenal primaries 1–2 with no fluorescence. Photographs by Scott Weidensaul.
DISCUSSION

This technique was developed for Barn Owls, and is described here primarily for Northern Saw-whet Owls. However, it appears to have wide applicability to many, if not all, species of owls. We and others have tested black UV lights on a variety of wild and captive North American owls, and all fluoresce. Eastern Screech-Owls (Megascops asio) exhibit a pattern and color almost identical to Northern Saw-whet Owls, as do Flammulated Owls (Otus flammuelus) (Jeff Smith, pers. comm.), while two captive adult Barred Owls (Strix varia) examined under black UV light showed a bright, violet-magenta fluorescence on newly molted remiges, but a complete absence on rectrices. Wild Barred Owls (classified as SY and ATY) examined in Washington State showed clear molt limits in the remiges with three generations easily visible in the ATYs (Jamie Acker, Dawn Garcia, and Stan Rullman; pers. comm.). A captive adult Great Horned Owl had weak fluorescence when initially examined, but a year later exhibited bright magenta fluorescence on newly molted remiges, perhaps as a result of a stronger UV source. An unknown-age Northern Pygmy-Owl (Glaucidium gnoma) examined in August in Washington State exhibited bright fluorescence on the underwing coverts and faint fluorescence on the base of the remiges (Jamie Acker, Dawn Garcia, and Stan Rullman; pers. comm.).

An HY Long-eared Owl (Asio otus), found freshly killed by a larger raptor in early December, had an even distribution of pale lavender fluorescence only at the base of the flight feathers where they had been covered by coverts, but exhibited strong fluorescence on the down feathers of the tarsi and flanks. An HY Long-eared Owl captured in November had a similar pattern, while an AHY Long-eared Owl netted at the same time had distinct flight feather molt limits under black UV light with new feathers fluorescing brightly. The molt limits were difficult to detect on the same bird using incandescent light. The fluorescence was purple-red shading to dark purple, and no fluorescence was noted on the rectrices, contour feathers or dorsal surfaces.

One concern is the effect of exposure to UV light on the eyes of both owls and banders. Ultraviolet wavelengths can cause tissue damage, although the long wave (UVA, 400-315 nm) radiation produced by commercial black UV lights is considered the least damaging of the three wavelength categories of ultraviolet light, and is found in most light sources, regardless of type. However, UVA bulbs may emit trace amounts of more damaging UVB radiation (Stellman 1998). There appears to be little information suggesting that brief exposure to UVA light experienced during normal banding operations would be harmful to owls, but caution is warranted. We make an effort to shield the eyes of owls during UV examination, often by shading the bird with a hand, and keep exposure as brief as possible.

A growing number of bird taxa have been shown to see wavelengths of light in the UV range (Bennett and Cuthill 1994, Bowmaker et al. 1997, Wilkie et al. 1998, Cuthill et al. 2000), and UV reflectivity has proven important for some birds in mate selection (Hunt et al. 2001, Pearn et al. 2001, Arnold et al. 2002, Hausmann et al. 2003) and hunting (Vittala et al. 1995, Koivula and Vittala 1999).

Recent research suggests that many taxa that appear monomorphic in visible light may be highly dimorphic when viewed in the UV range (Andersson et al. 1998). A recent plumage survey of ~1,000 nonpasserine bird species showed distinctive ultraviolet reflectivity, suggesting this visual ability may be widespread (Mullen and Pohland 2007).

Fluorescence differs from reflectivity, but the presence of abundant pigment in owl plumage that fluoresces brightly prompts the question: can the owls see this color and, if so, might it have a social or behavioral role, such as in mate selection? The absence of visible fluorescence on dorsal surfaces, head, or face of owls examined under black UV light argues against its use as a social signal, although the underwing surfaces where it is present would be observable in flight, such as during courtship rituals, and surfaces that reflect UV light may not fluoresce. The amount of UV light reflected by the moon is exceedingly low (the moon’s albedo is just 0.038; Henry et al. 1995), and may be below the threshold for visual detection, although many owls are active at dusk and dawn, when UV intensity may be greater. However, examination of the eyes of the Tawny Owl (Strix aluco) suggests owls lack the ultraviolet-sensitive/violet-sensitive (UVS/VS) cone class associated with ultraviolet vision (Bowmaker and Martin 1978, Cuthill et al. 2000). Boreal Owls (Aegolius funereus), under exper-
mental conditions, did not use ultraviolet markers to detect the presence of prey, as do diurnal raptors (Koivula et al. 1997). These factors in composite suggest ultraviolet fluorescence may not be a social cue, although further investigation is needed.

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Breeding Dispersal of a Burrowing Owl from Arizona to Saskatchewan

Geoffrey L. Holroyd,1 Courtney J. Conway,2 3 and Helen E. Trefry1

ABSTRACT.—We document a female Burrowing Owl (Athene cunicularia) that nested in Arizona and dispersed 1,860 km to Saskatchewan, where she successfully raised seven young during the same breeding season. The dispersal path between these two locations has not been documented previously. This is the longest distance ever recorded for breeding dispersal for any raptor within the same breeding season and possibly for any bird species.

Dispersal has important implications for population biology and evolution (Greenwood 1980. Wiens 2001). Breeding dispersal has been defined as movement between two successive breeding areas or social groups (Clobert et al. 2001). Breeding dispersal in birds is typically used to refer to movements between 2 years (Greenwood 1980, Greenwood and Harvey 1982), but within-year breeding dispersal can also occur when individuals move between two subsequent breeding attempts (Rosier et al. 2006).

Renesting (defined by Fankhauser 1964) has been documented for numerous species after an initial nesting attempt fails (Newton 1979). Second nesting attempts (those initiated after a successful attempt during the same breeding season, also termed double brooding) are rarely observed in raptors, and are thought to be uncommon due to the length of the breeding cycle (Marti 1969). The frequency of renesting and second nesting attempts is likely underestimated because the female must be individually marked and observed at both nests (Fankhauser 1964). Thus, instances of renests and second nests primarily have been those initiated at or near the initial nest site (Marti 1969, Millsap and Bear 1990, Marks and Perkins 1999). Distances moved between first and second nesting attempts within a breeding season (i.e., within-year breeding dispersal) are frequently not available and are likely underestimated for most, if not all, species.

Migration has been defined as the movement of an organism from one location to another either permanently (dispersal) or on a seasonal cycle (Roff and Fairburn 2001). Migration routes of Burrowing Owls (Athene cunicularia) have been poorly documented (Haug et al. 1993) due to low (1.5%) band encounter rates (Harman and Barich 2007). Burrowing Owls from the Canadian Great Plains migrate east of the Rockies, in a southeastern direction, based on 10 band encounters in the records of the U.S. Geological Survey's (USGS) Bird Banding Laboratory (BBL) through 2008, and nine owls with transmitters located in wintering areas (Holroyd et al. 2010). Encounters of 16 Burrowing Owls from British Columbia banded west of the Rocky Mountains revealed they migrated southwest to the U.S. Pacific Coast states (Holroyd et al. 2010).

We document two nesting attempts of a female Burrowing Owl within the same breeding season in widely separated locations (Arizona and Saskatchewan) that required crossing the Rocky Mountains in between the two previously known migration routes.

CHRONOLOGY OF 2003 BURROWING OWL NESTING EVENTS

We located a Burrowing Owl nest site at Davis-Monthan Air Force Base (32.2°N, 110.9°W) on 14 April 2003 during an intensive demography study in Tucson, Arizona, USA (Ogonowski 2007, Ogonowski and Conway 2009). A male owl was at the burrow entrance and, using an infrared video probe, we found a female 2.5 m below ground whose body posture was indicative of a bird sitting on eggs. On 27 April we observed a pair standing at the burrow entrance and, on 30 April, we trapped and banded both birds. The adult female Burrowing Owl was banded with a USGS band and an anodized black aluminum rivet band (Acraft Sign and Nameplate Co., Edmonton, AB, Canada) with vertical letters H
over M (hereafter HM). She had a vascularized brood patch and weighed 176 g, conditions indicative of an incubating female. We viewed the burrow entrance every 3–5 days over the next month. On 11 and 14 May we observed a pair; the female had a black Acrati band, but we were unable to read the alphanumeric code. On 18 May, we recorded one adult at the nest entrance and, on 21 May, using an infrared video probe, we detected one juvenile in the nest burrow. The juvenile was estimated to be 13 days of age, based on comparison to a Burrowing Owl photographic age guide modified from Priest (1997); this implies it was hatched on ~8 May suggesting that HM began incubating between 10 and 16 April using a 22-day incubation period (Conway et al. in review).

We observed only the male at the nest entrance on 25 May and, on 29 May, the same male was present. A new female was in attendance and subsequently trapped, at which time we observed three eggs. This new female had been banded on 22 April (black Acrati band with 9 vertical bar 7; hereafter 97) at a nest burrow where she had five eggs, and she was last seen there on 27 April. Female 97's first nest was 900 m from HM's nest and that nest failed between 27 and 30 April; one egg was found outside the burrow on 30 April and female 97 was not seen then or subsequently at her first nest burrow. This new pair (female 97 and HM's male) was still present at HM's nest burrow on 31 May, but on 13 June we found four abandoned eggs and no owls present. We found no owls on four subsequent nest visits in June. Female HM was seen next on 12 July 2003 in the Nashlyn Prairie Farm Rehabilitation Act pasture (49.1 N, 109.5 W) in southern Saskatchewan, Canada, when we were conducting brood counts in the area. We captured HM with a 46-year-old male and 7 young on 18 July 2003. Her brood patch was starting to grow in with pin feathers and she weighed 137 g. We confirmed both bands while she was in hand. This pasture is 1,860 km north of the nest at which she was banded in Arizona.

We estimated the oldest young to be 24–26 days of age on 18 July, while one young was much younger, based on the length of primary 9 and tail measurements (T. I. Wellicome, unpubl. data). We estimated HM's first egg was laid on 27 May based on a 22-day incubation period which started mid-way through the laying period, a 1.5-day laying interval between eggs, and a seven-egg clutch (Haug 1985, Wellicome 2005, Conway et al. in review).

**DISCUSSION**

The identification of this owl is certain because we trapped her in both locations and the U.S. Geological Survey and Acrati bands were confirmed in hand. This female Burrowing Owl laid and incubated a clutch (and hatched at least 1 nestling) in Tucson, Arizona and then moved 1,860 km north and successfully nested in Saskatchewan. We do not know which of the two females were present on 11 and 14 May so the departure date when HM left Tucson is unknown (we believe she likely departed just after her clutch hatched on 8 May). Female 97 could not have hatched the nestling (hatch date ~ 8 May) since she was involved in her own first nesting attempt until at least 27 April. Two other examples of females abandoning young nestlings and moving to initiate second nests with a new male have been observed at the Tucson study site (CJC, unpubl. obs.). This is the first time a second brood has been documented following long-distance dispersal by a Burrowing Owl.

Burrowing Owls have been documented with renests and second broods in California (Gervais and Rosenberg 1999, Catlin 2004, Rosier et al. 2006), in Florida (Millsap and Bear 1990), and in Arizona (Conway et al. in review). The intervals between fledging or failure of the first attempt and initiation of the subsequent attempt ranged from 16 to 150 days. Rosier et al. (2006) documented eight owls to disperse up to 54.1 km (mean = 14.9 km) but not all owls bred at the dispersal site that season. A. M. Fuentes Romero and M. Marquez Olivas (unpubl. data) documented a banded pair of Burrowing Owls in Texcoco, Distrito Federal, Mexico (19.5° N, 98.9° W) successfully producing two broods of three young each that hatched in March and December 2008. Catlin (2004) documented two pairs that produced three and four clutches after eggs were experimentally removed in California. These examples were from non-migratory populations and the females remained in the same nest burrow or only moved short distances (max = 54.1 km; Rosier et al. 2006) between nest attempts.

Encounters of Burrowing Owls banded in Canada indicate two migration patterns, one for Burrowing Owls east of the Rocky Mountains through the Great Plains, and the second for British Columbia along the west coast of North
America (Holroyd et al. 2010). The dispersal movement of the female Burrowing Owl reported in this paper crossed between these two migration 'corridors' from Arizona to Saskatchewan.

Our observation indicated this burrowing owl dispersed 1,860 km between two nesting attempts within the same breeding season. This is the longest distance ever recorded for breeding dispersal for any raptor (and possibly for any bird species) within the same breeding season. The female was not seen again the following year on either study site. The possibility of other species dispersing between two nesting attempts in the same breeding season has been indicated by stable isotope analysis (Hobson and Robbins 2009, Rohwer et al. 2009). We suggest the possibility of other examples of long distance breeding dispersal events within the same breeding season should be investigated. These dispersals have important implications for population genetics (Korfanta et al. 2005) and population dynamics (Clobert et al. 2001, Wiens 2001).

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High Density Nesting of Black-backed Woodpeckers (*Picoides arcticus*) in a Post-fire Great Lakes Jack Pine Forest

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ABSTRACT.—A stand-replacing fire in 404 ha of jack pine (*Pinus banksiana*) and mixed pine forest in Michigan’s Upper Peninsula in 2007 resulted in Black-backed Woodpeckers (*Picoides arcticus*) nesting at high density in 2008, the second possible nesting season post-fire. Nests were found within a 93-ha study area and a 19-ha stand (a subset of the 93-ha study area) in 199.5 survey hours concentrated in March-July. The 19-ha stand had six nests, a density of 0.31 nests/ha or 0.63 individuals/ha, while the 93-ha study area had 20 nests yielding 0.21 nests/ha or 0.42 individuals/ha. These nest densities are higher than previously reported in the literature for comparable stands, indicating a large influx of nesting woodpeckers post-fire. High nesting densities in this study may have resulted from: (1) optimal timing of the fire for wood-boring beetle exploitation of burned trees, (2) the discrete nature of burned habitat in the study due to impacts of salvage logging, or (3) our focus on regions of the burn where high nesting densities occurred, as the entire burned area (404 ha) was not included in nest density calculations. Received 23 April 2010, Accepted 28 December 2010.

The distribution of Black-backed Woodpeckers (*Picoides arcticus*) in the Upper Peninsula of Michigan is limited to relic glacial depression bogs, and boreal outwash plains occupying 7.3% of Michigan’s total forest area, widely interspersed within the ubiquitous deciduous forest matrix (Dickman and Leefers 2003). Black-backed Woodpeckers occur at low densities in these habitats and are irregularly detected; there were only 10 confirmed breeding records in seven Upper Peninsula counties during Michigan’s Breeding Bird Atlas of 1983–1988 (Evers 1991). However, Black-backed Woodpeckers have been shown to increase seven-fold in density and abundance following sporadic occurrence of wildfire (Dixon and Saab 2000). This led Hutto (1995) to propose burns may be source habitats and unburned forests may be sinks. This implies: (1) burns favor maximum reproductive performance, (2) newly augmented populations disperse from a burn following depletion of burn resources, and (3) populations wait out a “stasis-period” at low densities in sub-optimal, unburned forests, until a new fire prompts immigration to new high-quality habitat. Nappi and Drapeau (2009) found that nesting densities and abundance peak in the second year post-fire and rapidly decline after the third year because saproxylic insects used as prey require recently dead trees. This suggests an ephemeral relationship where fire, wood-boring insects, and woodpeckers peak and wane in accord.

On 29 April 2007, a controlled burn set 2 days previously in the Ottawa National Forest of Upper Michigan escaped control and heavily burned ~404 ha of mature jack pine (*Pinus banksiana*), mixed jack-red (*P. resinosa*)-white pine (*P. strobus*), and deciduous–coniferous forest on the Baraga Plains, ~22 km southwest of L’Anse, Baraga County, Michigan (centered at 46°35′20″ N and 88°36′56″ W). We made minor explorations of a selected area within the entire burn in June 2007 and increased the frequency of visits through fall and winter 2007–2008. We decided in March 2008
to investigate densities of nesting Black-backed Woodpeckers using a 93-ha subset of the 404-ha burn during the 2008 breeding season, the second opportunity for nesting (second year) after the fire. Our objectives in this paper are to report: (1) very high nest densities, and (2) a summation of general nesting phenology and site characteristics.

METHODS

We located three Black-backed Woodpecker nests within the burn in 2007 during limited surveys immediately following the fire. The 93-ha study area was delineated in early 2008 and two and three times weekly, 2- to 7-hr surveys were made on foot to locate as many Black-backed Woodpeckers and nests as possible. We slowly searched the study area for nests during each survey, bisecting the habitat in a series of transects spaced at 20- to 40-m intervals. When a Black-backed Woodpecker was located, we attempted to infer from its behavior whether it was (1) paired and (2) near an active nest. We recorded the following data when nests were located: tree species, tree diameter at breast height (DBH), nest height, nest orientation, tree status (killed by fire, snag, etc.), and latitude and longitude. We revisited previously located nests during successive surveys recording data on nest phenology for: start of nest excavation, first young heard, last young in nest, and first date of no nest activity. The entire 93-ha study area was not completely covered during each day's survey, but cumulative visits over the entire area ensured systematic sampling. The nature of the habitat with relatively small, discrete blocks of burned pines with little understory vegetation, set within a matrix of burned clear-cuts, made it relatively easy to keep track of our location in relation to woodpeckers. The desire to find all Black-backed Woodpecker nests in the study area and limited hours available prevented following any one pair or nest intensively. We conducted surveys from 7 January 2008 through 7 December 2009 with 40 surveys totaling 160 hrs concentrated in March through July; 199.5 survey hrs were accumulated in the total survey period of January–December. A period from 28 May through 3 June had no surveys at all.

We used circular statistics (Rao's spacing test, \(U\); mean vector length, \(r\)) following Rendell and Robertson (1994) for nest tree data to ascertain if nest entrance orientation was correlated with compass direction. Significance was set at \(P < 0.05\). Nest locations were also plotted, based on Global Positioning System (GPS) locations, to calculate accurate densities of nests within the study area (of known size). We were able to calculate the actual density of nesting individuals/ha in the 93-ha study area (and a 19-ha subset of the 93-ha study area where nests were densest) based on documentation of woodpecker pairs at each nest cavity.

RESULTS

Twenty active Black-backed Woodpecker nests were found in 2008 within the 93-ha study area (Fig. 1). Thirty percent of the 20 nests \(n = 6\) were confined to a discrete 19-ha subset of the 93-ha study area, and another was in a clear-cut just outside the 19-ha stand (Fig. 1). One active nest was also found during a 1-hr survey through a stand of mature jack pine ~1 km outside the burn and study area. The overall nest density for the entire 93-ha study area was 0.21/ha, while the 19-ha stand had a nest density of 0.31/ha and also included a successful Hairy Woodpecker (Picoides villosus) nest.

The first date of nest excavation was 24 March (Table 1). One nest failed before young were heard (4 Jun), two nests failed after young were heard (21–26 Jun) and 17 nests advanced to the stage of single large young visible in the nest entrance (16–26 Jun). No evidence of nest failure was observed at the 17 remaining nests during the next nest survey, and we projected fledge date estimates for each of the 17 nests, based on the median date between surveys (Table 1). The first young heard in nests were on 4 June and the last young observed in nests were on 29 June. The intermittent nature of visits to each nest (not all nests were visited each survey day), the non-intrusive observation methods, and the 7-day gap in late May and early June limited the exact delineation of nesting phenology.

Nest heights in the 93-ha study area ranged from 0.71 to 8.32 m with a mean ± SD of 3.18 ± 2.25 m. Nest tree diameter at breast height (DBH) ranged from 16.51 to 40.64 cm with a mean ± SD of 23.62 ± 7.82 cm (Table 1). Eighteen of 20 located nests (90%) were in jack pines, of which 77% were killed by the 2008 fire (Table 1). Orientation of nest entrances did not vary significantly with respect to compass direction, indicating nests were randomly distributed within a 360° field (Rao's \(U = 133.85\), \(P > 0.10\)); mean vector length was
also low, indicating nests were widely dispersed ($r = 0.228$, mean vector angle = 225.9°).

**DISCUSSION**

Prior to the 2008 burn, Black-backed Woodpeckers were present as rare permanent residents in the general burn area on the Baraga Plains, nesting in small numbers (single nests found in 1999 and 2000) in mature jack pine stands (Binford 2006). Our data indicate high densities of Black-backed Woodpeckers nesting in the 93-ha and 19-ha study areas in comparison to
TABLE 1. Black-backed Woodpecker nest parameters within a 93-ha study area consisting of burned mature pine forest on the Baraga Plains, Baraga County, Michigan. 2008. Projected June fledging dates indicate an estimated date of fledging ± half the number of days between last young heard and date of empty nest.

<table>
<thead>
<tr>
<th>Nest number</th>
<th>Date of discovery</th>
<th>Date of 1st young heard</th>
<th>Projected June fledging date (days)</th>
<th>Species of nest tree</th>
<th>Type of nest tree</th>
<th>DBH of nest tree (cm)</th>
<th>Orientation of nest opening (°)</th>
<th>Height of nest cavity (cm)</th>
<th>Nest success</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>21 Apr</td>
<td>4 Jun</td>
<td>24.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>19.05</td>
<td>156</td>
<td>1.82</td>
<td>Fledged</td>
</tr>
<tr>
<td>2</td>
<td>5 Jun</td>
<td>23 Jun</td>
<td>Failed</td>
<td>JP</td>
<td>Snag</td>
<td>22.86</td>
<td>0</td>
<td>7.31</td>
<td>Failed</td>
</tr>
<tr>
<td>3</td>
<td>12 May</td>
<td>10 Jun</td>
<td>24.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>25.4</td>
<td>117</td>
<td>8.32</td>
<td>Fledged</td>
</tr>
<tr>
<td>4</td>
<td>16 Jun</td>
<td>16 Jun</td>
<td>30.0 ± 1.0</td>
<td>JP</td>
<td>Dead</td>
<td>31.75</td>
<td>144</td>
<td>5.18</td>
<td>Fledged</td>
</tr>
<tr>
<td>5</td>
<td>21 Apr</td>
<td>4 Jun</td>
<td>17.5 ± 1.5</td>
<td>JP</td>
<td>DBF</td>
<td>24.13</td>
<td>269</td>
<td>1.52</td>
<td>Fledged</td>
</tr>
<tr>
<td>6</td>
<td>12 May</td>
<td>5 Jun</td>
<td>24.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>17.78</td>
<td>246</td>
<td>3.04</td>
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</tr>
<tr>
<td>7</td>
<td>14 Apr</td>
<td>5 Jun</td>
<td>17.5 ± 1.5</td>
<td>JP</td>
<td>DBF</td>
<td>17.78</td>
<td>104</td>
<td>3.65</td>
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</tr>
<tr>
<td>8</td>
<td>16 Jun</td>
<td>16 Jun</td>
<td>27.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>30.48</td>
<td>290</td>
<td>6.40</td>
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</tr>
<tr>
<td>9</td>
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<td></td>
<td>Failed</td>
<td>JP</td>
<td>KBF</td>
<td>22.86</td>
<td>223</td>
<td>4.87</td>
<td>Failed</td>
</tr>
<tr>
<td>10</td>
<td>14 Apr</td>
<td>4 Jun</td>
<td>17.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>16.51</td>
<td>237</td>
<td>1.95</td>
<td>Fledged</td>
</tr>
<tr>
<td>11</td>
<td>12 May</td>
<td>5 Jun</td>
<td>20.0 ± 1.0</td>
<td>JP</td>
<td>KBF</td>
<td>24.13</td>
<td>293</td>
<td>1.52</td>
<td>Fledged</td>
</tr>
<tr>
<td>12</td>
<td>12 May</td>
<td>5 Jun</td>
<td>17.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>24.13</td>
<td>244</td>
<td>1.16</td>
<td>Fledged</td>
</tr>
<tr>
<td>13</td>
<td>1 May</td>
<td>4 Jun</td>
<td>22.0 ± 1.0</td>
<td>JP</td>
<td>KBF</td>
<td>21.59</td>
<td>291</td>
<td>1.21</td>
<td>Fledged</td>
</tr>
<tr>
<td>14</td>
<td>4 Jun</td>
<td>10 Jun</td>
<td>30.0 ± 1.0</td>
<td>JP</td>
<td>KBF</td>
<td>24.13</td>
<td>250</td>
<td>0.71</td>
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</tr>
<tr>
<td>15</td>
<td>24 Mar</td>
<td>5 Jun</td>
<td>17.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>27.94</td>
<td>42</td>
<td>3.04</td>
<td>Fledged</td>
</tr>
<tr>
<td>16</td>
<td>14 Jun</td>
<td>14 Jun</td>
<td>24.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>30.48</td>
<td>225</td>
<td>5.18</td>
<td>Fledged</td>
</tr>
<tr>
<td>17</td>
<td>8 Jun</td>
<td>8 Jun</td>
<td>22.0 ± 1.0</td>
<td>WP</td>
<td>Snag</td>
<td>40.64</td>
<td>167</td>
<td>2.26</td>
<td>Failed</td>
</tr>
<tr>
<td>18</td>
<td>5 Jun</td>
<td>14 Jun</td>
<td>27.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>16.51</td>
<td>74</td>
<td>1.39</td>
<td>Fledged</td>
</tr>
<tr>
<td>19</td>
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<td>10 Jun</td>
<td>Failed</td>
<td>RP</td>
<td>Snag</td>
<td>20.32</td>
<td>152</td>
<td>0.93</td>
<td>Failed</td>
</tr>
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<td>20</td>
<td>21 Apr</td>
<td>16 Jun</td>
<td>24.5 ± 1.5</td>
<td>JP</td>
<td>KBF</td>
<td>26.67</td>
<td>47</td>
<td>4.87</td>
<td>Fledged</td>
</tr>
<tr>
<td>21</td>
<td>19 Jun</td>
<td>19 Jun</td>
<td>30.0 ± 1.0</td>
<td>JP</td>
<td>Snag</td>
<td>19.05</td>
<td>309</td>
<td>2.43</td>
<td>Fledged</td>
</tr>
</tbody>
</table>

* KBF = killed by fire, DBF = dead before fire, Snag = dead long before fire, Dead = dead (but not within burn area).
* Nest # 4 was outside the burn area.

the pre-fire forest in March–July 2008, the second breeding season post-fire. Greater food resources per unit of area may be available in burned rather than unburned forests as wood-boring beetles (Cerambycidae) capitalize on fire-killed or weakened trees, laying large quantities of eggs which hatch in the cambium as first-instar larvae the first year post-fire (Holsten et al. 1980). Wood-boring beetle larvae are one of the most common prey items of Black-backed Woodpeckers in unburned forests (Dixon and Saab 2000). However, our data support the conclusions of numerous researchers that Black-backed Woodpeckers occur at higher densities in burned forests (Heinselman 1973, Hutto 1995, Murphy and Lehnhausen 1998), most likely because of higher abundance of beetle larvae. We believe the densities in our study for both the 93-ha study area and 19-ha stand are the highest reported in the literature: 0.42 and 0.63 individuals/ha, respectively (2 birds/located nest). These values are 1.68 and 2.52 times higher than the highest reported density of 0.25 individuals/ha in a 67-ha plot of mature white spruce (Picea glauca) at a recent burn periphery (Murphy and Lehnhausen 1998). A study by Apfelbaum and Haney (1981) yielded a density of 0.1 individuals/ha higher than the density in our 19-ha stand (0.64 vs. 0.63), but the small area sampled (625 vs. 19 ha) and low number of individuals (4 vs. 12) lead us to discount this density from direct comparison. A more comparable 15 individuals/40 ha in uncut burned spruce in central Montana (Dixon and Saab 2000) gives a density of 0.38, slightly lower than the density in our 93-ha study area. Our data indicate a nest density nearly twice as high as recorded in severely burned spruce forest in Quebec (Nappi and Drapeau 2009). It is possible that burned jack pine provides a richer prey base than spruce, leading to higher nesting densities. Higher nest density in our study occurred in a stand of pure burned jack pine compared with stands of mixed pines (jack, white, and red).

Several factors may influence the densities in our study. Black-backed Woodpeckers were observed to do most of their foraging within the burned mature stands, but were also observed foraging outside those stands, indicating a larger...
area was being used than the 93 ha intensively studied. Conversely, we found an active Black-backed Woodpecker nest in a clear-cut 100 m outside the 19-ha stand and these birds moved into the 19-ha stand to forage. Prior to salvage logging in late April-early March 2008, the 19-ha stand of mature burned jack pine was actually a 35-ha stand (Fig. 1). Sixteen of the 35 ha were clear-cut at that time, creating the 19-ha stand studied. This sudden reduction of habitat early in the breeding season may have introduced an artificial constraint on Black-backed Woodpeckers using the burn, causing pairs to establish nests at higher densities in the remaining 19 ha. Hairy Woodpeckers were also observed displacing Black-backed Woodpeckers from foraging sites during eight of 13 interspecific contacts, partially supporting the observations of Villard and Beninger (1993) that Black-backed Woodpeckers may compete with other Picoides woodpeckers for food resources in a burn. Black-backed Woodpeckers were only observed to displace Hairy Woodpeckers five times, all within 50 m of an active Black-backed Woodpecker nest.

The earliest date of nest excavation (24 Mar) is slightly earlier than reported excavation phenologies (Dixon and Saab 2000). Continued monitoring after nests in the study area were located indicated an 85% projected fledging success rate during the second possible breeding season after the fire (2008). Nests were initially located on surveys at different stages during breeding development, precluding precise delineation of nesting phenology, but projected mean fledge dates in successful nests had a fairly high synchronicity with a standard deviation of ±1 days over a 14-day range. The high proportion of jack pines selected for nests may be misleading as a majority of nests located in the burn were in stands dominated by mature jack pine. Compass direction was apparently not a key factor in nest entrance placement, although the relatively small sample size may have masked statistical trends.

We believe the high nest densities in this study raise several intriguing questions beyond the scope of the present study. We do not know if high-density nesting, as found in this study, is actually the standard post-fire breeding strategy, or whether individual characteristics of this burn caused the unusually high density. Research that may have implications for the high nesting densities in our study, indicates that Picoides woodpeckers’ saproxylic insect prey are most abundant in trees of early stage decay-classes, limited to recently dead conifers (Saint-Germain et al. 2007). Timing of the fire immediately following snowmelt in early April, may have presented optimal resources to saproxylic insects at a critical point in their life history: following adult emergence 1-3 months after the fire, they were able to quickly exploit the high-quality, freshly-burned substrate, establishing high larval densities that could be used by Black-backed Woodpeckers in the second year post-fire. Burns that occur later in the summer or fall may miss the window for heavy insect colonization the first year after the fire, decreasing the probability that high larval loads are ever established, and limiting woodpeckers to larger range sizes and lower densities. It is also possible the burned habitat in our study area, chiefly mature jack pine forest focused by timber cutting into discrete stands, provided a rich but confined food source for both wood-boring beetles and woodpeckers.

Previous Black-backed Woodpecker studies have generally reported nest densities over the entire burned area regardless of where nests are actually distributed, implying a constant nest density per hectare even in unsuitable habitat. Where high-density nesting occurs, nest densities (not foraging densities) in this format do not reflect the actual clustering of Black-backed Woodpecker nests in a discrete region of a burn. A more precise approach, accurately describing the spatial proximity of nests, would: (1) calculate density via a “best fit” approach, delineating a burned area around which a maximum number of nests can be confined (as in this study); or (2) use spatial analysis (point pattern analysis) to correlate nests to an exact area. We believe factors influencing Black-backed Woodpecker nest site selection within a burn could be more easily identified using either of these methods.

We question if the source-sink model described by Hutto (1995) may have limited application to Black-backed Woodpecker dynamics in the Upper Peninsula (near the southern range terminus of the species), where the fire interval is high due to both the isolated geographical nature of pyrophilic boreal forests (surrounded by mesic deciduous forest) and anthropogenic fire suppression (Dickman and Leefers 2003). The fire response distance of Black-backed Woodpeckers in this region would have to be very great for burns to provide the only productive habitat, which are both too
infrequent and limited in size to support a high proportion of the total breeding population. Mature and old growth coniferous forests with large numbers of snags in early decay classes may sustain habitat alternatives in unburned forests (Nappi and Drapeau 2009). Burns in the Upper Peninsula of Michigan are likely the optimum habitat (a source), but moderate population-level replacement probably occurs outside of them, as suggested as an alternate model by Hutto (1995). Additional studies in a wide variety of burned habitats and geographic locations within the Black-backed Woodpecker’s range are necessary to further identify patterns in nesting density, specifically: (1) reasons for spatial clumping of nests in particular regions of burned forest, and (2) an evaluation of whether unburned forests are sinks, comparing productivity of Black-backed Woodpeckers in burned versus completely unburned old-growth boreal forests.

ACKNOWLEDGMENTS

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LITERATURE CITED


that were open on the ground, but with a layer of vegetation between 1 and 2 m above the ground. Egg success was related to arrival date, density of the highest vegetation layer, density of nests in a given area, and percentage of nests on the ground. Brown pelicans that arrived earliest appeared to choose more optimal nest-sites and had greater egg and hatching success. Received 12 August 2010. Accepted 21 December 2010.

Animals are distributed non-randomly within a given habitat due to the pressures of natural selection (Southworth 1977). Non-random distribution is the result of organisms selecting particular patches within their habitats and selection is presumed to be adaptive; organisms choosing optimal habitats will be more successful than those that do not (Martin 1998). Selecting an optimal nest-site by birds can have implications for nestling fitness and overall survival.

Brown Pelicans (Pelecanus occidentalis) are now reaching population levels along the Gulf Coast that were achieved prior to the widespread use of DDT as a pesticide (Schreiber and Risebrough 1972, Wilkinson et al. 1994). This species is now a common breeder in the southeastern United States, but little has been reported on its breeding biology along the Gulf Coast (Sachs and Jodice 2009) with no reports for Alabama.

Brown Pelicans, while historically commonly observed on the coast of Alabama, had not nested in the state (Imhof 1976) until four nests were discovered on Gaillard Island in 1983 (Wilkinson et al. 1994). As many as 5,000 breeding pairs have returned to Gaillard Island each year since 2003 (Roger Clay, pers. comm.). Our objectives were to: (1) investigate nest-site selection, and (2) the implications of nest-site selection on hatching and egg success of Brown Pelicans.

METHODS

Study Site.—This study occurred over two breeding seasons (2007–2008) at Gaillard Island, Alabama (30° 30' N, 88° 02' W). Gaillard Island is a man-made, dredge spoil island in Mobile Bay that is 2.6 km at its greatest width and 3.6 km at its greatest length. It is just east of Dog River and 17.7 km south of downtown Mobile (Robinson and Dindo 2009). There is a 6.1-m dirt berm perimeter completely around the island that protects it from storm surge and provides protected nesting habitats for numerous bird species. The dominant vegetation on the island is marsh elder (Iva frutescens) and cord grass (Spartina spp.). Brown Pelicans commonly nest in marsh elder on the island and many nest on the ground near vegetation. The southern end of Gaillard Island, comprising about 20% of the island, is used by Brown Pelicans for nesting, as much of the island is non-vegetated dredge spoil. Brown Pelicans typically arrive on Gaillard Island in late March and begin building nests in April. New nests can be found through June. Gaillard Island is the only known nesting site in Alabama for Brown Pelicans.

Field Methods.—Eleven sites (and quadrats) on Gaillard Island were selected in February 2007 and February 2008, prior to arrival of Brown Pelicans. Quadrats were chosen based on vegetation cover and the sites’ positions on the island. Vegetation density was ranked as: 0 = no vegetation (<2% cover above 0.5 m from the ground), 1 = low vegetation density (<30% cover), 2 = moderate vegetation density (30–60% cover), and 3 = high vegetation density (>60% cover). Sites were selected for each category inside and outside of the berm. Percent vegetation cover was estimated following Sneddon (1993). Quadrats (20 m²) were established at each of the sites in locations that represented the diverse vegetation cover differences and position on the island.

Each quadrat was divided into four vegetation layers: from the ground to 1 m, 1–2 m, 2–3.5 m, and 3.5 m to the top of the vegetation (Sneddon 1993). Percent cover at each layer for each quadrat was used in the statistical analysis. Seven variables were measured to examine their effects on egg and hatching success: date of arrival (Julian date), vegetation density (DV) of the layer <1 m (ground height DV), vegetation density of
TABLE 1. Eigenvalues, proportion of variance explained, and cumulative variance of principal components for Brown Pelicans nesting on Gaillard Island, Alabama.

<table>
<thead>
<tr>
<th></th>
<th>PC I</th>
<th>PC II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>3.439</td>
<td>2.132</td>
</tr>
<tr>
<td>Proportion of variance</td>
<td>0.491</td>
<td>0.305</td>
</tr>
<tr>
<td>Cumulative variance</td>
<td>0.491</td>
<td>0.796</td>
</tr>
</tbody>
</table>

the layer 1-2 m (low height DV), vegetation density of the layer 2-3.5 m (moderate height DV), vegetation density of the layer 3.5 m to the top of the vegetation (tall height DV), nest density (number of nests/m²), and number of nests on the ground (as a percent of total nests).

Pearson’s correlation was used to examine if year or position relative to the berm had an effect on hatching or egg success. A principal component (PC) analysis was performed using the above variables; principal components were selected for and used in regression analyses with egg success and hatching success. Quadrats one and four could not be used in this analysis as no nesting occurred in either. Pearson’s correlation was performed between each variable and each principal component to examine any relationships. A stepwise regression routine was performed to select a model that best fit the relationship between date of arrival and vegetation variables.

RESULTS

We observed 384 Brown Pelican nests and 852 eggs over two breeding seasons on Gaillard Island. The largest clutch size observed was three, and this was a common clutch size. Brown Pelicans nested primarily on the ground and in marsh elder; however, two nests were in the invasive Chinese tallow tree (Triadica sebifera). No nests were found at a height >2 m. Study year had no effect on egg (P = 0.144) or hatching success (P = 0.176). Principal component 1 (PC I) and principal component II (PC II) were chosen based on eigenvalues (Table 1).

Egg success ranged from 0.046 to 0.659 (Table 2) with a mean of 0.507 and had a significant and negative relationship with PC I (P = 0.006, R² Adj. = 69.0%, β estimate = -0.086 PC I). Hatching success ranged from 0 to 0.695 young hatched per laid egg (Table 2) with a mean of 0.539 and was significantly related to PC I (P = 0.002) and PC II (P = 0.027) (R² Adj. = 79.5%, β estimate = -0.091 PC I, -0.068 PC II). The relationship between hatching success and PC I was also negative.

Date of arrival ranged from no arrival (no nesting in the quadrat) to Julian day 161 (9 Jun) and the mean day of arrival was Julian day 125 (4 May) for those quadrats that had an arrival date (Table 2). The best regression routine selected two variables for the regression model: low height DV and the interaction between the first two vegetation layers (ground height DV X low height DV). Arrival date was significantly related to low height DV (P = 0.004) and the interaction between the two vegetation layers (P = 0.015).

DISCUSSION

PC II was a function of the vegetation layers in which Brown Pelicans were nesting and PC I was a function of those factors that did not directly involve the nesting vegetation layers (Table 3).

TABLE 2. Egg success (ES), hatching success (HS), Julian date of arrival (JD), percentage of nests on the ground (N oG), and vegetation cover in each layer (GH < 1 m, LH = 1-2 m, MH = 2-3.5 m, TH > 3.5 m) for each quadrat for Brown Pelicans nesting on Gaillard Island, Alabama.

<table>
<thead>
<tr>
<th>Quadrat</th>
<th>ES</th>
<th>HS</th>
<th>JD</th>
<th>NoG</th>
<th>GH</th>
<th>LH</th>
<th>MH</th>
<th>TH</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0.80</td>
<td>0.20</td>
<td>0.12</td>
<td>0.90</td>
</tr>
<tr>
<td>2</td>
<td>0.393</td>
<td>0.500</td>
<td>148</td>
<td>0.500</td>
<td>0.45</td>
<td>0.40</td>
<td>0.12</td>
<td>0.00</td>
</tr>
<tr>
<td>3</td>
<td>0.452</td>
<td>0.537</td>
<td>145</td>
<td>0.114</td>
<td>0.70</td>
<td>0.35</td>
<td>0.15</td>
<td>0.40</td>
</tr>
<tr>
<td>4</td>
<td>0.046</td>
<td>0.0</td>
<td>161</td>
<td>0.0</td>
<td>1.00</td>
<td>0.98</td>
<td>0.70</td>
<td>0.22</td>
</tr>
<tr>
<td>5</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0.90</td>
<td>0.02</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>0.535</td>
<td>0.677</td>
<td>113</td>
<td>0.979</td>
<td>0.84</td>
<td>0.57</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>7</td>
<td>0.562</td>
<td>0.635</td>
<td>113</td>
<td>1.000</td>
<td>0.90</td>
<td>0.73</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>8</td>
<td>0.639</td>
<td>0.576</td>
<td>108</td>
<td>0.834</td>
<td>0.97</td>
<td>0.70</td>
<td>0.15</td>
<td>0.02</td>
</tr>
<tr>
<td>9</td>
<td>0.659</td>
<td>0.695</td>
<td>117</td>
<td>0.510</td>
<td>0.87</td>
<td>0.47</td>
<td>0.35</td>
<td>0.09</td>
</tr>
<tr>
<td>10</td>
<td>0.649</td>
<td>0.588</td>
<td>112</td>
<td>0.620</td>
<td>0.70</td>
<td>0.40</td>
<td>0.12</td>
<td>0.30</td>
</tr>
<tr>
<td>11</td>
<td>0.626</td>
<td>0.646</td>
<td>112</td>
<td>0.711</td>
<td>0.95</td>
<td>0.60</td>
<td>0.11</td>
<td>0.01</td>
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</tbody>
</table>
TABLE 3. Coefficients for Pearson's correlation analysis between principal components and variables for Brown Pelicans nesting on Gaillard Island, Alabama.

<table>
<thead>
<tr>
<th></th>
<th>PC I</th>
<th>PC II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Julian date of arrival</td>
<td>0.929**</td>
<td>-0.039</td>
</tr>
<tr>
<td>Ground height DV</td>
<td>-0.206</td>
<td>0.916**</td>
</tr>
<tr>
<td>Low height DV</td>
<td>0.107</td>
<td>0.937**</td>
</tr>
<tr>
<td>Moderate height DV</td>
<td>0.764*</td>
<td>0.565</td>
</tr>
<tr>
<td>Tall height DV</td>
<td>0.628</td>
<td>-0.239</td>
</tr>
<tr>
<td>Nest density</td>
<td>-0.788*</td>
<td>0.195</td>
</tr>
<tr>
<td>Nests on ground</td>
<td>-0.961**</td>
<td>0.003</td>
</tr>
</tbody>
</table>

* $P < 0.05$ ** $P < 0.001$

Both egg and hatching success increased with earlier arrival dates, lower vegetation density in the layer 2-3.5 m above ground, higher nest density, and more nests on the ground. Hatching success increased as the vegetation density in the layer 1-2 m above ground and vegetation density in the layer 1-2 m above the ground decreased. Arrival date was positively related to vegetation density between 1 and 2 m above the ground. It was negatively related to the interaction term of the first two vegetation layers (ground height DV x low height DV). The vegetation density between 1 and 2 m above the ground increased as arrival date became later and the interaction between the first two vegetation layers decreased, indicating those arriving first chose sites with little to no vegetation on the ground but some vegetation above the ground. It is not surprising that year had no effect on egg or hatching success.

The study was conducted for 2 years which is not sufficiently long to draw conclusions regarding year effects on Brown Pelican nesting ecology. The more successful Brown Pelicans on Gaillard Island arrived earliest and selected sites with less dense vegetation within 1 m of the ground. This provided more room to nest on the ground, but with some cover above the ground. Lower vegetation densities were selected first and nests in those areas were more successful. This could be related to size of Brown Pelicans. They must incubate eggs, sit on the nest when not incubating, and land on the nest or take flight from the nest (Shields 2002). Dense vegetation does not allow some or all of these actions. Clumsy landings of Brown Pelicans can crush eggs or knock them from nests (Maxwell and Kale 1977). These problems were minimized by nesting in less dense vegetation. Vegetation in which nesting occurred ceases to be a factor when nests were on the ground. Egg and hatching success increased significantly in those quadrats with a high percentage of nests on the ground. Another benefit to those nesting on the ground is predator avoidance. Nesting Brown Pelicans from ground nests are able to leave the nest and return earlier than those nesting in vegetation above the ground – as early as 3 weeks after hatching (Shields 2002). These nestlings could leave the nest to avoid predation (from avian predators) at a much earlier age than those from nests above the ground. Selecting for ground nests, but with vegetation above ground level provides thermoregulatory benefits (Grant 1982) and cover from avian predators. Gaillard Island is free of mammalian and reptilian predators. The only predators of Brown Pelican eggs and young are gulls and wading birds. Ground nests under the cover of vegetation hides eggs and chicks from predators hunting from the air. Another factor that may affect nest-site selection and productivity is age of the nesting birds. We collected no data on age, but Blus and Keahey (1978) have shown that older Brown Pelicans have the greatest nest success. A longer study would be needed to show these effects.

Brown Pelicans are now flourishing along the Gulf Coast of Alabama. However, with development of coastal areas, the ephemeral nature of spoil islands, natural disasters, and man-made disasters in the Gulf of Mexico, their future is uncertain. This study provides insight into nest preference and the relative success rates of microhabitats at nest sites. This study also provides important baseline data for future studies on the breeding ecology of Brown Pelicans in the Gulf of Mexico.

ACKNOWLEDGMENTS

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LITERATURE CITED


Nest, Eggs, and Nesting Behavior of the Gray Trembler
(Cinclocerthia gutturalis) on St. Lucia, West Indies

Joshua B. LaPergola, Jennifer L. Mortensen, and Robert L. Curry

ABSTRACT.—Few descriptions exist of the nesting behavior of the Gray Trembler (Cinclocerthia gutturalis), and the only nest description of this species seems incongruent with what is known about nesting behavior of other species of Mimidae. We report the first definitively described nest of the Gray Trembler in St. Lucia, West Indies in June–July 2007. We observed construction of, incubation at, and feeding of nestlings in an open-cup nest, similar in architecture to nests of other mimids, contradicting previous reports that Gray Trembler nests are domed, constructed of dried grass and on top of palm (Cocos nucifera) trees. Received 18 May 2010, Accepted 27 October 2010.
Ramphocinclus brachyurus (Temple et al. 2006, 2009).

The tremblers (Cinclocerthia spp.), in particular, are poorly known. Since their description in the mid-19th century, the Brown Trembler (C. ruficauda) and Gray Trembler (C. guturalis) have been periodically lumped and split; the genus included at least two species in the late 19th century (Cory 1886), was monotypic in the early 20th (reviewed by Storer 1989), and split again later that century (AOU 1991). Recent morphological (Storer 1989) and molecular (Hunt et al. 2001) phylogenetic analyses support recognition of two distinct trembler species. Presently, the Martinique and St. Lucia populations are recognized as Gray Trembler and all other Lesser Antillean island populations are recognized as Brown Trembler (AOU 1998, Cody 2005). Only two studies of Brown Trembler natural history exist, both from Dominica: Zusi (1969) investigated feeding ecology and Markowsky et al. (1994) studied the function of the species’ namesake trembling wing display. No formal studies have examined Gray Trembler behavior and/or ecology, and we suggest that published descriptions of the nest and eggs of this species are suspect.

Nearly all mimids are known to construct open-cup nests with a few exceptions (Cody 2005). Outliers include Sage (Oreoscoptes montanus) and Brown (Troxostoma rufum) thrashers which are occasional ground-nesters (Cody 2005), cavity-nesting Pearly-eyed Thrasher (Margarops fuscatus) (Arendt 2006) and, according to published accounts, Gray Trembler. Cody (2005:481) and Keith (1997:108) describe Gray Trembler nests as “domed” with both nest descriptions based on Danforth (1935:74), who reported a St. Lucian Gray Trembler nest as, “a domed structure made of dry grasses, with the entrance at the side” containing eggs (not described). Danforth’s second-hand account was based on a description recounted by a resident of St. Lucia. In contrast, a “cup-shaped” Brown Trembler nest sent from Dominica was described by Bond (1941:372). Quoting his correspondent, the nest was “situated in a fairly high coconut palm at the base of a frond, in the little hollow where it grew out of the trunk”; and “although a nest, similarily situated, was found in St. Lucia (Cinclocerthia ruficauda macrorhyncha), the usual nesting site of this species would seem to be in the cavity of a tree or in the hollow stump of a tree-fern.” Whether Bond or another person observed the nest on St. Lucia is unclear. Bond’s (1971:170) field guide reiterated that Brown Tremblers (considering, at the time, Gray Tremblers as conspecific) nest “in a cavity of a tree or tree fern, or at the base of a palm frond.”

A source for description of Gray Trembler eggs is also ambiguous. Bond (1971:170) described the eggs of “Trembler” as “greenish-blue” with a clutch size of 2-3 without specifying a source. Subsequent authors (e.g., Raffaele et al. 1998, Cody 2005) appear to have applied Bond’s description to the eggs of both Gray and Brown tremblers, although Bond did not distinguish between the species.

Our objective is to report unequivocal descriptions of the nest structure and eggs of a Gray Trembler on St. Lucia, West Indies documented by photographs. We also discuss the validity of prior reports of the nesting biology of this species and its sister taxon, the Brown Trembler.

STUDY AREA

Our observation of a Gray Trembler nest occurred during study of the White-breasted Thrasher (Ramphocinclus brachyurus) within the Mandelé Range, a 680-ha fragment of regenerated dry forest on the east coast of St. Lucia, West Indies between the towns of Dennery and Praslin (Anthony and Dornelly 2008). The vegetation consists of littoral woodland and scrub species, transitioning into deciduous tropical dry forest away from the coast, and interspersed with subsistence agriculture and charcoal pit clearings (Temple 2005). A large portion of the Mandelé Range is currently being developed into a multi-use resort, resulting in dry forest destruction and landscape fragmentation (Mortensen 2009). The Gray Trembler nest observed was in a 47.6-ha forested plot on the development property.

OBSERVATIONS

Nesting Phenology.—We observed a Gray Trembler carrying a stick to the top of an understory tree ~15 m from a forest edge, adding the stick to a nest already under construction at 0850 hrs on 24 June 2007; the nest possessed a well-formed cup by 27 June 2007. We observed (using a digital video camera attached to a long stick) three eggs in the nest on 2 July 2007. Later that day, we observed an adult Gray Trembler incubating the eggs. The last day of egg observation was 13 July 2007, and the first
nestling performance was 16 July 2007 with no checks performed during the interim. We estimated from size and appearance that the trembler nestlings hatched on 15 July 2007, based on our experience observing >100 nesting attempts by closely related White-breasted Thrasher. Thus, the incubation period of this nest was ~14 days. The last day we observed nestlings was 25 July, and the nest was empty on 30 July 2007. The nest stage was a minimum of 11 days if the nestlings hatched on the date we estimated. However, we saw no evidence of fledging (i.e., we did not hear fledglings calling from outside the nest nor observe any adult trembler behavior suggesting that fledglings were in the immediate vicinity of the nest). The trembler nest was possibly depredated, given the high rate of failure for the open-cup and similarly placed White-breasted Thrasher nests in the same habitat (Mortensen 2009).

We observed two Gray Trembler fledglings at different locations within the study site on 27 and 28 June 2007. If we assume a nesting cycle of ~25 days (likely an underestimate due to uncertainty about clutch initiation date, hatching date, and date of failure/fledging), the known Gray Trembler breeding season extends, at least, from the beginning of June until the end of July.

Nest Description.—The Gray Trembler had a bulky, open-cup, not domed nest (Fig. 1A, B). The cup of the nest consisted mostly of dead leaves and, to a lesser extent, thin twigs, and lacked the cleanly woven cup-structure of rooflets and other plant fibers typical of some other members of the catbird and Caribbean thrasher clade (RLC, pers. obs.). The outer portion of the nest consisted of larger twigs with dead leaves between the twigs surrounding the cup. The nest was in the forking branches just below the top of the crown in a ~4.5-m tall Myrtia deflexa (Myrtaceae) tree.

Eggs, Hatching Success, and Brood Reduction.—The Gray Trembler nest contained three light greenish-blue eggs (Fig. 1B), nearly identical in appearance to eggs of other members of the catbird and Caribbean thrasher clade, especially to those of the White-breasted Thrasher (JBL, pers. obs.). All three eggs hatched. One of the three nestlings disappeared from the nest between 23 and 25 July 2007, but the parents continued to feed the remaining two nestlings.

We used two still-frames from one of our videos and morphometric data from the literature to estimate sizes of the three eggs. Storer (1989) reported a mean beak from nostril length of 31.38 mm for female St. Lucian Gray Trembler. We used this value and ImageJ (Abramoff et al. 2004) to estimate the length of a small stick in the nest visible in a still-frame with a Gray Trembler, which we assumed to be female, incubating (Fig. 1A). We used this reference to estimate the length and width of the three eggs in another still-frame. Estimated dimensions (length x width) of the three eggs were 19.37 x 16.73 mm, 21.32 x 16.63 mm, and 19.91 x 15.61 mm, yielding mean (± SD) length of 20.20 ± 1.01 mm and width of 16.32 ± 0.62 mm. However, these estimates have limited accuracy because of the assumptions inherent in our methodology.

Parental Behavior.—Parents fed the nestlings a combination of arthropods, small vertebrates, and fruit. Specifically identified food items included centipedes (Scolopendra spp.) and dwarf geckos (Sphaerodactylus spp.). We did not band any adult tremblers near the active nest, and we observed no more than two adults concurrently in the vicinity of the nest. One trembler, on more than one occasion, flew at and pecked the video camera. However, even with the camera positioned <1 m from the nest, at least one adult continued to incubate during the egg stage and provision chicks during the nestling stage.

DISCUSSION

Our observations of St. Lucian Gray Trembler nestling biology question the accuracy of historical nest descriptions, while highlighting the necessity of rigor in field studies of avian reproduction. We propose two reasons for the discrepancy between our observations and previously published Gray Trembler nest descriptions: (1) initial descriptions of a Gray Trembler's nest were inadequate and open-cup nests are typical for the species, or (2) the disparity between accounts reflects natural variation in the species, as recently observed in another Caribbean mimid, the Black Catbird (Melanoptila glutirostris), which can nest (a) in open, cavity-like depressions in dead or living trees, (b) between peeling bark and tree trunks, and (c) in typical, mimid open-cup nests in branches (JBL, unpubl. data). Some variation in nest structure exists among and within species in the Mimidae, including Sage and Brown thrashers, species that occasionally nest on the ground (Cody 2005), and Pearly-eyed Thrasher, which often nests in secondary cavities (Arendt 2006). However, construction of a domed nest for Gray
Tremblers would suggest a radical departure from the simpler open-cup nest typical of most mimids. We suggest Danforth's (1935) original second-hand description may have resulted from misidentification of the owners of the nest in question. Resident species on St. Lucia that build domed or otherwise covered nests include St. Lucia Black Finch (Melanospiza richardsoni), Lesser Antillean Bullfinch (Loxigilla noctis), Black-faced Grassquit (Tiaris bicolor), Antillean Euphonia (Euphonia musica), Bananaquit (Cocerda flaveola), and St. Lucia Oriole (Icterus laudabilis) (Keith 1997).

Our observations establish unequivocally the color (greenish-blue) of Gray Trembler eggs, but the accuracy of our estimates of egg dimensions is questionable. Our length and width estimates are smaller than those for Brown Trembler (C. ruficata ruficata) eggs from Dominica (length: 25.91 ± 0.93 mm and width: 19.49 ± 0.08 mm; n = 3 eggs; from the collection at the Western Foundation of Vertebrate Zoology, catalogue number 120.066; René Corado, pers. comm.). Adult St. Lucian Gray Tremblers are on average larger than Dominican Brown Tremblers (Storer 1989), which suggests our measurements under-

FIG. 1. Gray Trembler nest on St. Lucia. (A) Adult trembler incubating. (B) Eggs and nest structure visible between incubation bouts (photographs by J. B. LaPergola).
estimate actual Gray Trembler egg size because egg mass (and, thus, egg size) correlates with adult body mass in passerines (Martin et al. 2006). However, to our knowledge, the Gray Trembler egg dimensions we present represent the only available for the species and offer a basis for comparison with any egg dimension data collected for Gray Tremblers in the future.

Our description of the Gray Trembler’s nest stresses the importance of accurate data for conservation efforts. The similarity in physical appearance of the observed nest and eggs of the Gray Trembler on St. Lucia, a species of least concern (BirdLife International 2009), to the nests and eggs of its endangered relative, the White-breasted Thrasher, suggests nests containing eggs cannot be attributed to one or the other of these species without identifying the birds attending the nest.

The Gray Trembler is not presently considered at risk, but it experiences similar extrinsic and intrinsic conditions as other species restricted to islands. Island endemics, compared with species having continental ranges, comprise a disproportionately large percentage of threatened and endangered avifauna (Temple 1985). Gathering basic natural history data for the trembler and other poorly known species can inform management and help avert conservation problems. For example, the White-breasted Thrasher was recently discovered to be a facultative cooperative breeder with three or more individuals contributing care at many nests (Temple et al. 2006). This social system, which is well known in several other mimids (e.g., Galápagos mockingbirds, Nesomimus spp.; Curry and Grant 1990), can strongly influence effective population size and population persistence. Whether helpers are present at Cinclocerthia nests remains unknown. We hope the accurate, unequivocal nest and egg descriptions provided here will facilitate future study and clarify details of the Gray Trembler’s natural history.

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Behavior of Warbling Vireos Ejecting Real and Artificial Cowbird Eggs

Todd J. Underwood\textsuperscript{1,2,3} and Spencer G. Sealy\textsuperscript{4}

\textbf{ABSTRACT.}—We videotaped nine ejections of real \((n=5)\) and artificial \((n=4)\) Brown-headed Cowbird \((Molothrus ater)\) eggs by Warbling Vireos \((Vireo gilvus)\). All eggs were ejected within 6 min. There were no significant differences in time used for any ejection behavior by egg type, although artificial eggs were probed longer before ejection. Eight vireos ejected the cowbird egg using visual cues only because none sat on its nest before ejection. One male ejected the cowbird egg after sitting on the nest for a few minutes; consequently, both visual and tactile cues were available for its decision to eject the cowbird egg.

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Most vireos identified the cowbird egg by sight and, in most cases, rapid ejection of the cowbird egg precluded the possibility of using tactile cues. Grasp-ejection was the only ejection method confirmed for real and artificial eggs. Two male vireos ejected cowbird eggs at two nests, which is the first documentation of successful ejection by male Warbling Vireos, and the third cowbird host for which males are known to eject cowbird eggs. The ability of males to eject cowbird eggs has important implications for the evolution of ejection behavior. \textit{Received 10 August 2010. Accepted 7 January 2011.}

High reproductive costs incurred by hosts of obligate brood parasites (Lorenzana and Sealy 1999, Davies 2000) favor evolution of defenses against the parasitic egg, such as egg ejection, egg
burial, and nest desertion (Rothstein 1990). Egg ejection appears to be the most effective and efficient defense against parasitism (Rothstein 1975a, Peer et al. 2005, Underwood and Sealy 2006a), although it is sometimes associated with costs, especially for small hosts (Lorenzana and Sealy 2001, Martin-Vivaldi et al. 2002). Experiments documenting egg ejection have been conducted for many years (e.g., Rothstein 1975a); however, previous knowledge about ejection behavior relied on rare anecdotal observations of ejection by hosts and a few intense observational studies involving experimental parasitism (Sealy and Neudorf 1995). More recently, use of video cameras has revealed additional details regarding ejection behavior. The method by which hosts eject eggs has been ascertained for several species (Moksnes et al. 1994, Soler et al. 2002, Underwood and Sealy 2006a, Rasmussen et al. 2009). However, for most species, less is known about whether the male or female ejects the parasitic egg (Sealy and Neudorf 1995, Soler et al. 2002, Honza et al. 2007), the behavior leading to egg ejection (Antonov et al. 2008, 2009), and the time required to discriminate and eject foreign eggs (Sealy and Bazin 1995, Antonov et al. 2008). We report details of videotaped observations of Warbling Vireos (Vireo gilvus) ejecting real and artificial Brown-headed Cowbird (Molothrus ater) eggs that offer insight into the experimental use of different types of eggs, egg discrimination behavior, and the evolution of ejection behavior.

METHODS

Our study was conducted at Delta Marsh, Manitoba (50° 11’ N, 98° 23’ W) where we located Warbling Vireo nests from May to July 1998 and 1999, Warbling Vireos, at 15 g with a tomaill bill length of 17.2 mm, are the smallest known ejecters of cowbird eggs and are capable of both puncture- and grasp-ejection (Sealy 1996, Underwood and Sealy 2006a). Incubation in this sexually monomorphic species is by both males and females (Gardali and Ballard 2000); thus, males have the opportunity to be directly involved in egg discrimination.

Warbling Vireo nests were experimentally parasitized as soon as they were available (i.e., during laying or incubation) because nest stage does not influence the response of Warbling Vireos to parasitism (Sealy 1996, Underwood and Sealy 2006a). We videotaped Warbling Vireos ejecting real \((n = 5)\) and artificial \((n = 4)\) cowbird eggs in conjunction with two other experiments (Underwood and Sealy 2006a, b). We calculated the length of time vireos were involved in ejection behaviors, whether only visual cues or a combination of visual and tactile cues were used by vireos for cowbird egg discrimination, and whether males ejected eggs.

Single real cowbird eggs were experimentally added to vireo nests in 1998. One nest was parasitized during the laying stage, whereas four nests were parasitized during the incubation stage. Real cowbird eggs were painted over with non-toxic, acrylic paints to match the appearance of a cowbird egg as a control for various treatments of painted eggs as part of a study of the parameters of egg discrimination (Underwood and Sealy 2006b). Vireos ejected these painted eggs at about the same frequency as real, unpainted cowbird eggs (Sealy 1996, Underwood and Sealy 2006b). Vireo nests in 1999 were experimentally parasitized with a single artificial cowbird egg made of plaster and painted with non-toxic, acrylic paints to match the appearance of real cowbird eggs (Underwood and Sealy 2006a). All of these nests were parasitized during the incubation stage. Individuals at these nests previously ejected real eggs in several treatments as part of another study (Underwood and Sealy 2006b).

Nests in both years were videotaped for 1 hr to record ejection behavior after a cowbird egg had been added. We recorded for each ejection the time from egg addition until ejection (time until ejection), the time from a vireo’s arrival at the nest until ejection (time for ejection), the time from the start of probing the cowbird egg until ejection (probing period), and the actual time the vireo probed (time probing; Table I). The probing behavior of Warbling Vireos involved a combination of pecks and tremble-thrusting movements prior to ejecting cowbird eggs. Tremble-thrusting (i.e., pushing of the bill into the nest with a vibrating motion) is used by some songbirds to turn or rotate eggs during normal incubation (Deeming 2002). We were unable, however, to consistently differentiate these behaviors or the strength of pecks (sensu Soler et al. 2002, Antonov et al. 2008) because the deep nest cups and height of the vireo nests precluded a clear view of the bird’s head some of the time. Thus, we used probing behavior to describe any pecking or bill-thrusting movement directed into the nest cup.
TABLE 1. Time (sec) for Warbling Vireos to respond to real and artificial Brown-headed Cowbird eggs experimentally added to their nests. "Time until" variables represent the time from egg addition until the vireos have responded. All measurements represent mean ± SE (sec) for each variable.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Real cowbird egg (n = 5)</th>
<th>Plaster cowbird egg (n = 4)</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time until eject</td>
<td>232.0 ± 64.5</td>
<td>328.8 ± 126.5</td>
<td>-0.73</td>
<td>0.49</td>
</tr>
<tr>
<td>Time until return</td>
<td>171.0 ± 50.0</td>
<td>164.3 ± 55.5</td>
<td>0.09</td>
<td>0.93</td>
</tr>
<tr>
<td>Time for ejection</td>
<td>60.8 ± 38.5</td>
<td>164.5 ± 74.4</td>
<td>-1.32</td>
<td>0.23</td>
</tr>
<tr>
<td>Probing period</td>
<td>51.0 ± 37.0</td>
<td>161.8 ± 74.4</td>
<td>-1.43</td>
<td>0.20</td>
</tr>
<tr>
<td>Time probing</td>
<td>16.8 ± 6.5</td>
<td>115.5 ± 40.6</td>
<td>-2.40</td>
<td>0.09</td>
</tr>
</tbody>
</table>

*Equal variances not assumed.

and, presumably, toward the eggs. We compared the time used for ejection of real cowbird eggs to that for artificial cowbird eggs because the latter may be more difficult to eject and may not reflect ejection times of real eggs (Martín-Vivaldi et al. 2002, Prather et al. 2007). We also recorded whether vireos sat on their nest prior to egg ejection to identify the potential use of tactile and visual cues in egg discrimination. The method of egg ejection was identified, where possible, for each egg type. We also ascertained, where possible, whether males were responsible for egg ejection. Males were identified based on whether they sang before ejection because there is no evidence female Warbling Vireos of the eastern subspecies sing (Howes-Jones 1985a, b).

RESULTS

Warbling Vireos ejected both real and artificial cowbird eggs within 6 min on average after experimental parasitism (Table 1). Much of the delay until ejection was due to the vireos' absence from the nest, but once a vireo returned to the nest, egg ejection was rapid (Table 1). There were no significant differences in length of time for any ejection behaviors when vireos ejected real eggs compared to artificial eggs (Table 1). However, vireos on average spent six times as long probing artificial cowbird eggs compared to real cowbird eggs. No host eggs were damaged (e.g., missing or punctured) in any of these ejections.

All vireos immediately looked into their nest when they first arrived after experimental parasitism and within 30 sec began probing inside it (mean ± SE = 6.7 ± 3.4 sec). Four of five vireos ejected real cowbird eggs without sitting on the nest. The remaining vireo sat on the nest a few minutes before ejecting the cowbird egg, although it probed within the nest before sitting. All four vireos ejected artificial cowbird eggs without sitting on the nest. Thus, vireos used only visual cues for egg discrimination in eight ejections, whereas in one ejection both visual and tactile cues were available for egg discrimination.

The method of egg ejection was confirmed at four nests. Two real cowbird eggs were ejected by grasp-ejection and, as previously reported (Underwood and Sealy 2006a), two artificial cowbird eggs were ejected by grasp-ejection. The exact method of ejection (grasp- or puncture-ejection) could not be confirmed at three nests parasitized with real eggs and at two nests parasitized with artificial eggs due to the position of the vireos during ejection. The video evidence, however, indicated these eggs were ejected with the bill.

Male Warbling Vireos ejected cowbird eggs at two nests (one each in 1998 and 1999). Four minutes after experimental parasitism at nest 1998-38, a vireo landed above the nest, looked into it and then settled on the nest. Several seconds later, the vireo began singing, which identified it as a male. The male sat on the nest for ~3 min where it mixed bouts of singing with probing inside the nest. After a final bout of probing for 6 sec, the vireo ejected the cowbird egg 3 min and 33 sec after arrival. Five minutes after experimental parasitism at nest 1999-75, a vireo landed on the nest branch and, after probing inside the nest twice, it sang. This male sang intermittently as it continued to probe or peck inside the nest until finally ejecting the cowbird egg 6 min and 23 sec after arrival.

DISCUSSION

Warbling Vireos rapidly ejected cowbird eggs from their nests. Cowbird eggs differ in two parameters (size and spot pattern) from Warbling Vireo eggs (Underwood and Sealy 2006b), making them strongly non-mimetic. Non-mimetic
eggs are rejected faster than mimetic eggs by many hosts of hooed parasites (Underwood and Sealy 2002, Antonov et al. 2008). Cowbird eggs are non-mimetic to the eggs of most ejector species and many of these species eject most cowbird eggs within 24 hrs (Rothstein 1976, Sealy and Bazin 1995, Sealy and Neudorf 1995). However, few studies have measured the actual time until ejection of the cowbird egg to permit comparison of the speed of ejection; most measure the ejection frequency at 24-hr intervals. Baltimore Orioles (Icterus galbula) also ejected cowbird eggs rapidly with 88% ejected within 1 hr (Sealy and Neudorf 1995), but Eastern Kingbirds (Tyrannus tyrannus) only ejected 14% within 1 hr (Sealy and Bazin 1995). Sealy (1996) recorded only 25% ejection of real, unpainted cowbird eggs ($n = 16$) within 1 hr in the same population of Warbling Vireos compared to 100% ejection ($n = 9$) in this study. Differences in nest stage at time of experimental parasitism cannot explain this discrepancy in time until ejection because nest stage does not influence this interval in Warbling Vireos (Sealy 1996, Underwood and Sealy 2006b). The rapid ejection of real and artificial cowbird eggs in this study is likely because the paints applied to these eggs made them appear more strongly non-mimetic and, for artificial eggs, their response to repeated parasitism may have been faster, as it is by Eurasian Blackcaps (Sylvia atricapilla) (Honzá et al. 2007).

We found no significant differences in any measure of ejection behavior by egg-type. However, vireos probed artificial eggs about six times longer than real eggs before ejecting them. The lack of a significant difference in probing time was likely due to the relatively small sample sizes of the two egg-types for comparison. The difference in probing time seems large, but a probing time of $\sim$2 min to remove an artificial cowbird egg compared to 17 sec to remove a real cowbird egg does not likely represent true difficulty in egg ejection. For example, Baltimore Orioles took an average of 11 min to puncture eject real cowbird eggs (Sealy and Neudorf 1995). The difference in ejection experience of Warbling Vireos exposed to real versus artificial eggs had the potential to influence most of the time of ejection behaviors (e.g., Honza et al. 2007). Experienced vireos took longer to eject artificial cowbird eggs than non-experienced vireos to eject real cowbird eggs. This non-significant difference suggests that egg material may have a stronger influence on ejection time than experience does for Warbling Vireos.

Warbling Vireos damaged none of their own eggs when ejecting artificial cowbird eggs (Underwood and Sealy 2006a). A few other hosts, in comparison, were more likely to damage their own eggs while ejecting artificial eggs (Martin-Vivaldi et al. 2002, Prather et al. 2007), or were unable to eject artificial eggs made with certain materials (Rothstein 1976, 1977; Prather et al. 2007; Antonov et al. 2009). The well developed grasp-ejection ability of Warbling Vireos, confirmed in this study, likely explains why this small host had little apparent difficulty ejecting artificial eggs (Underwood and Sealy 2006a). Most species that have difficulty ejecting artificial eggs are small and are likely puncture-ejectors (Martin-Vivaldi et al. 2002, Prather et al. 2007, Antonov et al. 2009; but see Honza and Maskát 2008). Larger cowbird hosts, such as American Robin (Turdus migratorius) and Gray Catbird (Dumetella carolinensis), apparently have no difficulty ejecting artificial eggs (Rothstein 1976, Lorenzana and Sealy 2001).

Warbling Vireos apparently eject cowbird eggs based on visual cues. Sealy (1996) observed four instances of ejection of experimental cowbird eggs by Warbling Vireos. Females always looked into the nest and attempted to eject the cowbird egg without settling on the nest to incubate. A host may use tactile stimuli detected during incubation to identify a foreign egg by size (Rothstein 1982), as suggested for Rufous Horneos (Furnarius rufus) and American Robins (Rothstein 1982, Mason and Rothstein 1986). Sealy (1996), out of seven observed ejection attempts, noted only one (male) Warbling Vireo settling on the nest before attempting to eject a cowbird egg. These results were confirmed in this study. Most vireos ejected the cowbird egg before settling on the nest. Only at one nest did the male vireo eject the egg after settling on the nest. Thus, most vireos identified the cowbird egg by sight and, in most cases, rapid ejection of the cowbird egg precluded the possibility of using tactile cues. Rothstein (1982), in contrast, suggested the quickest ejections by robins were due to use of both visual and tactile stimuli. The different behavior of male Warbling Vireos may be due to a lack of experience in ejecting cowbird eggs, as has been suggested for male Baltimore Orioles (Sealy and Neudorf 1995), and not use of different stimuli.
One of five real cowbird eggs was ejected by a male Warbling Vireo in 1998 and, in 1999, one of four model cowbird eggs was ejected by a male. Thus, at least 22% of ejections were by males, which is the first confirmed documentation of male Warbling Vireos ejecting cowbird eggs. This represents a lower estimate of the proportion of ejections by males, however, because we relied on song to identify them. The two ejections by males had the longest times until ejection, which confirms Sealy and Neudorf’s (1995) suggestion that males are less experienced ejecters and Honza et al.’s (2007) observations that female Eurasian Blackcaps eject more quickly than males.

Sealy (1996) observed two male Warbling Vireos attempt unsuccessfully to eject cowbird eggs, but his other observations implicated ejection only by females. Ejection by males has also been observed in two other Brown-headed Cowbird hosts, Gray Catbirds and Baltimore Orioles (Sealy and Neudorf 1995). Alexander Wilson recorded ejection of Brown Thrasher (Toxostoma rufum) eggs by a male catbird (summarized in Sealy and Neudorf 1995), but male ejection in this species has not been confirmed because catbirds are sexually monomorphic. Sealy and Neudorf (1995) predicted that species where males incubate or feed females at the nest are the most likely to have evolved egg ejection by males. Ejection by male Warbling Vireos supports this prediction because males also incubate (Gardali and Ballard 2000). Experiments with a few host species of Common Cuckoo (Cuculus canorus) also support this prediction. Soler et al. (2002) found that in species where males also incubated, both males and females ejected artificial cuckoo eggs, but in those where males did not incubate, only females ejected them. This trend has been supported in studies of three additional cuckoo hosts where both males and females ejected cuckoo eggs (Lee et al. 2005, Honza et al. 2007) and where only females ejected (Požgayová et al. 2009). Previously, females have generally been assumed to be solely capable of ejection because in many species they conduct most activities at the nest (e.g., Rothslein 1975b). However, in Brown-headed Cowbird hosts, identifying which gender ejects has been difficult because most species that eject are not sexually dimorphic (Sealy and Neudorf 1995). Only two species of ~20 known ejecter species (Underwood 2003, Peer and Sealy 2004), Baltimore Orioles and Bullock’s Orioles (Icterus bullockii), are strongly sexually dimorphic; most observations of ejection have not been made in populations that are uniquely color marked. Thus, involvement of males in cowbird egg ejection may have been underestimated. Ejection by males has theoretical implications because ejection by both males and females should increase the spread of the ejector trait in a population (Rothslein 1975b, Kelly 1987, Sealy and Neudorf 1995).

ACKNOWLEDGMENTS

We thank C. M. McLaren and R. M. Underwood for field assistance. We also thank the staff of the Delta Marsh Field Station (University of Manitoba) for providing logistical support and the Portage Country Club, Delta Waterfowl and Wetlands Research Station, and private landowners who permitted us to work on their property. This study was funded by grants from the Natural Sciences and Engineering Research Council of Canada to SGS and a post-graduate fellowship from the University of Manitoba to TJU.

LITERATURE CITED


Conspecific Egg Destruction by a Female Cerulean Warbler

Than J. Boves,1,3 David A. Buehler,1 and N. Emily Boves2

ABSTRACT.—Conspecific egg destruction is an adaptive behavior that has typically evolved in multi-brooded, polygynous, or colonial avian species, and can be difficult to observe. We describe the first case of egg destruction in the Parulidae, which consists of mostly single-brooded and socially monogamous species. In this case, a female Cerulean Warbler (Dendroica cerulea) destroyed 5-day old eggs at a conspecific’s nest. This act was likely committed to secure a breeding opportunity with a high quality male or to decrease local competition for resources. There is also the possibility this behavior may have been pathological and not adaptive. Received 15 September 2010. Accepted 14 December 2010.

Destruction of eggs by conspecific adults has been documented in many avian species (e.g., Pieman and Belles-Isles 1987, Brown and Brown 1988, Hannsen et al. 1997). Conspecific egg destruction is generally considered adaptive and may occur when individuals are attempting to: (1) gain breeding opportunities with conspecifics that were previously mated to others (a sexual strategy), (2) gain resources through cannibalism (an exploitation strategy), (3) decrease competition for local resources (e.g., food or nest sites), or (4) manipulate the number or gender of offspring (only applicable when parents are responsible for the egg destruction) (Hrdy and Hausfater 1984). Egg destruction by birds occurs mainly in polygynous, colonial, or cooperatively-breeding species where the behavior is usually explained in a sexual or limited resource context. Great Reed Warblers (Acrocephalus arundinaceus) (Hannsen et al. 1997), House Wrens (Troglodytes aedon) (Quinn and Holroyd 1989), Green-rumped Parrotlets (Forpus passerinus) (Bonebrake and Bessinger 2010), and Marsh Wrens (Cistothorus palustris) (Pieman and Belles-Isles 1987) are among those species where individuals have been observed destroying, or have been inferred to have destroyed, conspecific eggs. Additionally, typically monogamous, solitary members of Troglo-dytiidae and Mimidae have been documented engaging in heterospecific egg-destroying behavior (Belles-Isles and Pieman 1986).

The Parulidae consists of mostly monogamous, single-brooded species that construct their own nests (Perrins 2004). These life history traits do not seem appropriate for evolution of conspecific egg destruction behavior because it appears best-suited for species that have high potential for breeding opportunities with multiple mates (e.g., Great Reed Warblers) or have limited availability of nest sites (e.g., House Wrens). We found no documentation of egg destruction by members of Parulidae in the literature. Cerulean Warblers (Dendroica cerulea) are insectivorous Nearctic-neotropical migratory members of Parulidae. Female Cerulean Warblers build cup-shaped nests in the canopy of deciduous forests of the eastern United States (Hamel 2000). We describe a case of conspecific egg destruction by a Cerulean Warbler and discuss the potential significance of this behavior.

METHODS

This event occurred in the North Cumberland Wildlife Management Area in Campbell County, Tennessee, USA (36°21'23.5"N, 84°18'08.4"W). This area is at an elevation of ~900 m and consists predominantly of mixed mesophytic forest with oak (Quercus spp.), maple (Acer spp.), hickory (Carya spp.), and tulip poplars (Liriodendron tulipifera) as the dominant tree species. We estimated, through intensive spot-mapping and nest-searching throughout the breeding season, Cerulean Warbler territory density at 1.3 pairs/ha on the 10-ha forest stand where the nest was located. This density is slightly above average in this part of the Cumberland Mountains (TJB, unpubl. data). The forest stand was occupied by a high proportion of young males (second-year birds). We captured and banded 23 male Cerulean Warblers in this stand from 2007 to 2010, 43% of which were second-year birds; across the rest of the Cumberland Mountains, only 28% of captures were second-year males (TJB, unpubl. data).

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Mayfield nest survival in this stand was the lowest among eight stands that we monitored from 2007 to 2010 (37% vs. 61% for seven other stands combined).

**OBSERVATIONS**

We watched a female Cerulean Warbler (hereafter Female A) between 1230 and 1405 hrs EST on 19 May 2010 aggressively attack an incubating female Cerulean Warbler (hereafter Female B) and destroy eggs in the nest. We found this nest on 10 May 2010 during the egg-laying stage, most likely after one egg had been laid (based on timing of behavioral observations at the nest). The nest was 16 m high in a cucumber magnolia (*Magnolia acuminata*). We observed Female B incubating for the first time on 15 May 2010; the egg destruction occurred on the fifth day of incubation. Female B’s mate was a fourth-year male banded in 2008 which had returned to this approximate location each of the following two breeding seasons. We monitored the interactions through a Kowa TSN-821 spotting scope equipped with a 2Q-60X eyepiece. We also attached a Nikon Coolpix P5100 digital camera to the scope and recorded much of what is described. The video is available at http://www.youtube.com/watch?v=rq2zUSVVhAs.

We were able to distinguish between the two females involved because Female B appeared to be a typical female Cerulean Warbler while Female A possessed several distinctive characteristics including a light breast band (which we have seen in other female Cerulean Warblers, but it is relatively unusual) and darker than normal streaking on the sides and flanks. The female-female interactions began while Female B’s mate was fighting with another male nearby (it is unknown if this male was paired). Female A was observed watching the male-male interactions and became physically involved in the fights several times (including tumbling to ground with the 2 males), while Female B remained on her nest. Female A also behaved in a manner reminiscent of a territorial male, repeatedly flicking her wings.

Female A approached to within 3 m of the nest where Female B was incubating on three occasions over a 10-min period as the two males interacted aggressively. Female B chased Female A from the nest tree on each approach. On the fourth approach, Female A moved within 1 m of the nest. Female B again chased Female A, however Female A did not retreat; instead the two birds fell to the ground together, their feet extended and clasped together for several seconds. This same interaction occurred three more times over the next 10 min, after which Female B returned to the nest to incubate. Two min later, Female A flew directly at Female B while she was on her nest. Female A used her feet to grab the wing of Female B and hung upside-down under the nest for several seconds until Female B flew off and the two birds tumbled to the ground together. Similar interactions were repeated five times; each time Female B was pulled or struck off the nest, tumbled to the ground with Female A, and then returned to incubate. After the sixth instance where Female A displaced Female B, we observed Female B sitting in a low sapling with one of her wings drooping slightly.

Subsequently, Female B did not return to her nest; Female A returned twice and simply looked into the nest. However, on her third trip to the abandoned nest, Female A stuck her head into the nest and made several pecking motions which were accompanied by the sound of eggs being punctured (heard from the ground below). Female A then flew and 10 min later returned, repeated the puncturing motions, and also appeared to ingest/drink something from inside the nest (possibly yolk from broken eggs). Female A returned to the nest 5 min later, once again appeared to consume something, and then wiped her beak on the side of the branch. Female A returned once more (1 min later) and perched next to the nest for 30 sec, looking around vigilantly. Female A then flew and we observed no activity at the nest for the next hour. We returned to the nest every 1–3 days for the next 30 days and did not observe another bird at the nest or in the nest tree. We observed the banded male singing in the same territory many times, and observed him feeding fledglings on 6 July 2010, but no other nest was found and neither female was observed again. The nest was still intact as of 6 July 2010.

**DISCUSSION**

Egg destruction is rarely observed and it is difficult to infer the adaptive nature (or lack thereof) of this behavior. The female Cerulean Warbler that destroyed the eggs of a conspecific could have done so as: (1) an adaptive sexual strategy, (2) a strategy to reduce local competition for resources, (3) an exploitation strategy, or (4) a pathological behavior with no adaptive value. The male occupying this territory helped raise a brood
successfully in both 2008 and 2009 in an area with relatively high rates of nest failure. Thus, Female A may have destroyed the eggs in an attempt to mate exclusively with this high-quality male. Cerulean Warblers are predominantly monogamous, but evidence of clustered territoriality or semi-coloniality (Oliarnyk and Robertson 1996, Roth and Islam 2007) and occasional polygyny exists. We observed six males feeding nestlings at simultaneous nests (of 100 males banded and over 250 nests monitored) from 2007 to 2010 in the Cumberland Mountains. It is possible that Female A was either a secondary mate of the banded male, or wanted to become his mate and committed egg destruction to improve her chances of breeding exclusively with him. Similar causes of egg destruction and infanticide in the highly polygamous societies of Great Reed Warblers and House Sparrows have been documented (Hannsen et al. 1997, Veiga 2004).

Female A may also have attempted to decrease local competition for resources by destroying the eggs. Food availability may have been low and Female A was attempting to decrease competition for that limited resource. Nests also contain limited resources (e.g., spider webbing), but none of the nest material was used after the egg destruction, so this is an unlikely explanation. We did observe Female A return to the nest after destroying the eggs and apparently consume yolk, but resource exploitation seems an unlikely explanation for the behavior because nutritional gain was probably exceeded by the costs of the behavior (e.g., risk of injury and energy expended). Female A may also have destroyed the eggs to reduce the number of young Cerulean Warbler nestlings/fledglings near her nest because a reduction in density of young may attract fewer predators to the area (Gunnarson et al. 2006).

Conspecific egg destruction by Cerulean Warblers may be adaptive, but it may also be pathological with no adaptive value. Female A possessed unusual characteristics including a slight breast band, some streaking on her belly, sides, and flanks, and behavior that mimicked male aggression (wing flicks and using her feet to grip Female B). Few female Cerulean Warblers that we have observed display these traits (<1% of females display breast bands or behave in this manner; TJB, pers. obs.). Egg destruction has not been documented in Parulidae despite the family being well-studied, and this case may be an aberration. However, Cerulean Warblers may be unique as a semi-colonial parulid, and they have been studied much less than many other parulid species. No previous study has documented egg predation or alternative causes of nest failure. Thus, conspecific egg destruction may be more common than we currently acknowledge.

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LITERATURE CITED


Harpie Eagle-Primate Interactions in the Central Amazon

Bryan Bernard Lenz1,3 and Alaercio Marajo dos Reis2

ABSTRACT.—We describe the successful predation of a black-bearded saki monkey (Chiropotes satanas chiropotes) by a Harpy Eagle (Harpia harpyja) in the Brazilian Amazon and briefly recap two past Harpy Eagle-primate predation interactions. The physiological limitations that raptor anatomy places on individuals during predation attempts are considered along with escape behaviors used by primates to exploit these limitations to increase their chances of survival. In particular, we focus on primate flight paths and startle vocalizations. Received 18 October 2010. Accepted 14 January 2011.

Predation by Harpy Eagles (Harpia harpyja) and predation on primates are rarely observed events. Raptor predation on primates can have strong impacts on primate group size and composition (e.g., Crowned Eagles [Stephmoetus coronatus]; Struhsaker and Leakey 1990), even at rates as low as one successful kill per year (Janson 1992). Botched attacks can potentially be fatal for raptors (e.g., Jones et al. 2006) and, as a result, what happens during predation interactions also has evolutionary significance for raptor species apart from the obvious benefits of the successful capture of prey. The importance of these events, in concert with how rarely they are witnessed, makes it crucial that each observation is carefully reported so that, over time, knowledge of raptor-primate interactions during predation events can be accumulated.

The objectives of this paper are to: (1) describe the successful predation of a juvenile female black-bearded saki monkey (Chiropotes satanas chiropotes) by a Harpy Eagle, and (2) discuss what these observations suggest about predator and prey strategies. More specifically, we focus on the physiological limitations of raptors and the way primate prey might adapt their flight paths and vocalizations to exploit these limitations. We also discuss two past Harpy Eagle-primate interactions and note two observations of Harpy Eagles with primate carcasses.

OBSERVATIONS

All observations were made in continuous, closed canopy terra firme forest at the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, Brazil. This study site has been described in detail by Gascon and Bierringard (2001).

Successful Predation Event.—The successful predation of a juvenile female black-bearded saki occurred during primate surveys on 21 February 2010 at 02:21:21.2 S, 60:06:45.2 W in undisturbed forest at the Dinoma Ranch of the BDFFP; the canopy height was ~30 m. The Harpy Eagle left the monkey on the ground before later returning for it, providing us with the rare opportunity to closely examine the pre-consumption carcass of a Harpy Eagle kill. At 09:11 hrs. during his approach to the site, the first observer heard the alarm calls of the Red-throated Caracara (Lherla americana) followed by a single loud black-bearded saki scream. This saki call was followed by standard black-bearded saki alarm calls from multiple individuals and the alarm calls of several White-throated Toucans (Ramphastos tucanus). Another saki scream was heard on or near the ground 15–25 sec after the first scream and a 1-m tall sapling was seen shaking as the observer arrived. An adult male Harpy Eagle flew from the ground at this location to perch 5 m above the ground in an understory tree 30 m distant.

At 09:25 hrs the Harpy Eagle flew away. The Red-throated Caracaras continued to alarm call while diving at the eagle from above as it took flight. We located the tip of a broken Harpy Eagle tail feather and the body of a large juvenile female saki lying on its side on the ground. There were two sets of puncture wounds on the saki, one from each of the eagle’s feet, and no other apparent wounds, although blood was coming from the anus. The wounds indicate the eagle attacked
from the saki's left side, grabbing the head and chest with its left foot and the lower half of the animal with its right foot. The anterior end of the monkey contained four punctures: the outer toe punctured the dorsal side of the neck at the spinal column, the middle toe entered the right side of the neck at the jugular, the inner toe entered the right side of the ventral thorax, and the hallux pierced the left side of the ventral thorax. The two punctures in the thorax formed a mirror image 30 mm below the collar bone at the location of the heart. Harpy Eagles typically make between two and four punctures to secure the posterior end of their prey, but the posterior end contained only one visible puncture on the right flank that was 60 mm anterior to the hip joint. We may have missed a posterior puncture(s) as they can be difficult to locate quickly because they can close without external hemorrhaging (Tania Sanioetti, pers. comm.).

We noticed the Harpy Eagle staring intently at us during our examination of the saki, moving its head side-to-side and up-and-down, from a perch 15 m high and 10 m distant. We hid in hope of seeing the eagle return to the kill but abandoned this effort after 20 min. We relocated the eagle perched 8-10 m up in the understory and 20-25 m from the carcass as we left the area. The Harpy Eagle flushed when we were within 15-20 m and flew ahead of us in the understory in the same direction in which we were walking. After moving forward 40 m in the understory, the Harpy suddenly flew into the canopy and made a 180-degree turn, returning to the area of the kill.

The saki was attacked while traveling in the smaller (5 individuals) of two subgroups (~18 individuals total). Typical black-bearded saki alarm calls began following the first loud scream at 0911 hrs. The smaller subgroup moved to the location of the larger subgroup, 40 m from the location of the attack, where together they alarm called vigorously until 0935 hrs (24 min). Individuals then gradually moved away until all alarms ceased (0946 hrs) and all individuals appeared to have left the area.

We infer the first scream was emitted by the individual that was attacked during an unsuccessful arboreal attempt. As it screamed we believe the monkey jumped 20–25 m to the ground, successfully eluding the eagle's grasp. We did not see the apparent terrestrial strike, but it appeared to be accompanied by another scream from the saki because it was at the location of this scream that we saw the sapling shaking immediately following the second scream and from which the Harpy Eagle flew from the ground. We believe that all wounds occurred during the second attempt and that this attempt was fatal.

Predation Attempts with Uncertain Outcomes.—

The second and third Harpy Eagle-primate interactions, involving another black-bearded saki and a red howler monkey (Alouatta seniculus), occurred in the last 25 years while one of the authors (dos Reis) worked on a variety of projects at the BDFFP. The second interaction was a Harpy Eagle attack on a black-bearded saki where the eagle attempted to capture an arboreal saki at one of the BDFFP’s continuous forest research sites, Cabo Frio. The monkey screamed at the moment of attack, jumped to the ground, and climbed 1–2 m up an understory tree where it remained. The eagle landed 15–25 m distant and surveyed the area while also studying the observer. As the observer left he heard another scream during what was likely a second attack with an unknown outcome.

During the third incident, an attempt on an arboreal red howler monkey at the continuous forest research site of Km41, the howler made an atypical vocalization at the moment of the attack and swung beneath the horizontal branch on which it was standing, briefly hanging upside down while the eagle passed over the top. The howler then returned to the top of the branch and ran towards its terminal end, moving to a neighboring vine-filled tree where it hid in thick vegetation with the rest of its group. The eagle perched 30 m distant and again surveyed the area, including the observer. As the observer left the area he heard another atypical howler vocalization, likely during a second attempt. The two vocalizations made by the howler during this encounter have not been heard by the observer (dos Reis) before or since (a total of 25 years). The outcome of this interaction is also unknown.

Post-capture Observations.—The final two observations, made from a truck on the large dirt road (ZF-3) used to access many of the research camps, were of Harpy Eagles that already had monkey carcasses. In the first, a Harpy Eagle was observed on top of a dead red howler monkey, using its beak to remove the howler's hair, which was placed in a single pile next to the body. The eagle flushed upon the approach of the vehicle but likely returned as the carcass was gone when the truck returned. The second observation was of a
TABLE 1. Primate prey of wild Harpy Eagles.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aotus</td>
<td>sp.</td>
<td>Robinson 2007</td>
</tr>
<tr>
<td>Ateles</td>
<td>paniscus</td>
<td>Ford and Boinski 2007</td>
</tr>
<tr>
<td>Callicebus</td>
<td>discolor, hoffmannsi</td>
<td>Aguiar da Silva 2007, de Luna et al. 2010</td>
</tr>
<tr>
<td>Saguinus</td>
<td>midas</td>
<td>Robinson 1994, Ford and Boinski 2007</td>
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<tr>
<td>Saimiri</td>
<td>boliviensis, sciureus</td>
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</table>

* Only partial post-crania were recovered but four species are likely given the quantity and size of the remains.

perched individual with the body of what appeared to be a black-bearded saki draped over the branch below it. The eagle did not flush and did not appear to be consuming the saki.

**DISCUSSION**

Harpy Eagles have been reported to prey on a number of primates (Table 1). We add a new species, C. s. chiropotes, to this list. Most Harpy Eagle-primate interactions are inferred through identification of primate remains at Harpy Eagle nests or through observations of Harpy Eagles that already have a primate carcass. There are three reports that detail the actual interaction between an attacking Harpy Eagle and its primate prey. Eason (1989) observed a Harpy Eagle attacking a group of red howler monkeys at the edge of an oxbow lake. The monkeys detected the approaching eagle well before it arrived, alarm called, and jumped to a vine tangle as the eagle glided towards them with its talons extended; a male howler then pursued the eagle until it left the area. Peres (1990) described a Harpy Eagle that attacked and killed a roaring male red howler monkey that was vocalizing on the periphery of its group. The eagle attacked the howler from behind and it seems the Harpy Eagle was not detected until it successfully struck the howler monkey. Martins et al. (2005) observed a Harpy Eagle dropping the dead body of a male bearded saki monkey (Chiropotes utahicki) in mid-flight and infer the monkey fought back because, when they recovered the carcass, it was clutching feathers in each hand. Our observations differ from these reports because, of the two cases that provide details of the actual attack, in one instance the Harpy Eagle was detected early in its approach (Eason 1989) and in the other it likely was not detected until after its strike (Peres 1990). The monkeys in the three cases that we report did not appear to detect the Harpy Eagle until the individual being attacked saw the raptor at the last moment because there were no alarm calls or reactions to the eagles until the startling vocalization at the instant of the first attempt. The anti-predator strategy in the attacks that we describe is likely different than in the cases described by Eason (1989) and Martins et al. (2005) due to the different detection times.

Our observations permit consideration of the potential physiological limitations of Harpy Eagles during an attack and the ways primate anti-predator behaviors exploit them. Raptors have highly focused binocular vision that creates "tunnel vision" and requires them to move their heads to track prey (Land 1999). Anatomical constraints greatly limit head movements during an attack, resulting in a limited ability to make in-flight focal adjustments (Shifferman and Eilam 2004). Prey movements at 90 degrees to the attack plane can be particularly difficult for a raptor to track with predator success rates decreasing to 0% for Barn Owls (Tyto alba) (Shifferman and Eilam 2004, Ilany and Eilam 2008). The effectiveness of this flight path (Ilany and Eilam 2008) for escape from fast approaching predators...
might also be inferred from the number of animals that are known to dodge sideways when faced with a predator at close range: song birds (Lima 1993, Kullberg et al. 2000, Lind et al. 2002, Lind et al. 2003), and ostriches, rheas, and gazelles (Farina et al. 2005).

Studies of prey flight paths tend to involve terrestrial prey and neglect another 90 degree escape path: fleeing straight down from the attack. Both saki monkeys in our observations selected this flight path when they jumped, as did the howler monkey when it swung to the underside of the branch. The number of primates that drop or rush down to lower levels of the canopy or even jump to the ground during last-second flight would seem to suggest this flight path also reduces raptor success rates (e.g., guenons [Cercocebus]; Shultz 2001, Corderio 1992; howler monkeys [Alouatta]; Eason 1989, this study; mangabeys [Lophocebus]; Arlet et al. 2009, sakis [Pithecia]; de Luna et al. 2010; bearded sakis [Chiroptera]: this study; tamarins [Saginus]; Heymann 1990, Peres 1993). Raptors likely will not shift their flight paths down to capture prey that jump from horizontal branches not only because of the difficulty of tracking prey moving at 90 degrees, but also because a downward adjustment risks a potentially fatal collision with the branch.

Most primate vocalizations that accompany interactions with predators are alarm calls intended to alert conspecifics or to prevent an attack before it begins by discouraging the predator (summarized by Wheeler 2008). Primate vocalizations that may serve as startle responses, however, are rarely discussed. Startle responses are abrupt changes in prey behavior meant to cause instantaneous responses in predator behavior to interfere with completion of the attack (Sargent 1990). These behaviors are used only after primary defense mechanisms have failed (Robinson 1969a, b; Edmunds 1974) and they are "novel, rare, conspicuous, anomalous and/or threatening" (Sargent 1990: 235) so predators are unlikely to habituate to them. The goal is to create a moment of hesitation (a startle) that provides additional opportunity for escape. The saki scream that we heard was a startle response because it was given at the moment of attack, it was very loud (conspicuous), and it is rare. The junior author (dos Reis) has heard this saki call only three times in 25 years, twice during the attacks reported here and once during a possible predation attempt during a previous study with 605 contact hours with black-bearded saki monkeys (Sarah Boyle, pers. comm.). The howler vocalization was likely also a startle response as the observer (dos Reis) has not heard this vocalization outside of this encounter and it also meets the other criteria.

The extent to which startle vocalizations and the 90 degree downward flight path aided in escape is not clear, but the Harpy Eagle was at least required to make multiple attempts in all three observations. This suggests these last-minute primate anti-raptor defenses are successful in exploiting raptor weaknesses to increase the probability of survival by extending the predator-prey interaction.

ACKNOWLEDGMENTS

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LITERATURE CITED


Common Raven Predation on the Sand Crab

Paul Hendricks1,2 and Lisa M. Hendricks1

ABSTRACT.—We observed three Common Ravens (Corvus corax) hunting for live sand crabs (Emerita analoga) during low tide on Netarts Spit, Oregon in mid-August 2010. One raven successfully extracted four crabs in five attempts during a 5-min period. The ravens hunted on a large sandy beach near the upper margin of the swash zone (the area covered by active wave action); the focal bird extracted buried crabs using an initial thrust of its bill into the sand to flip sand aside, and then followed with two or three additional jabs before removing a crab from the sand. Extracted crabs were mature females, and the egg masses they carried appeared to be the target of the raven’s attentions. Low tides in late summer appear to be particularly favorable conditions for profitable and successful hunting of sand crab by ravens. This is the first description of the method by which ravens hunt live crabs of any species, and is further evidence of the ability of ravens to exploit seemingly novel and hidden food resources.

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The variety of foods documented in the diet of Common Ravens (Corvus corax), and the methods ravens use to obtain food, are extremely diverse; almost anything of nutritive value that can be captured, picked up, or stolen through use of the bill or feet is likely to draw the attention of ravens once it is perceived (Heinrich 1989, 1999; Ratcliffe 1997; Boartnan and Heinrich 1999). Ravens inhabiting some coastal areas are afforded many opportunities to capture intertidal invertebrates; coastal ravens at limes supplement their vertebrate diet with a variety of invertebrates, including polychaete worms, echinoderms, mollusks, and crustaceans, as well as coralline algae and sea weeds (Beni 1946, Ewins et al. 1986, Marquiss and Booth 1986). Remains of crabs (Hyas and Carcinus spp.) that occupy rocky, muddy, and sandy habitats in exposed or protected areas (such as estuaries) have been documented in regurgitated raven pellets recovered from British islands (Ewins et al. 1986, Marquiss and Booth 1986). However, the techniques used by ravens to capture crabs have not been described, nor have crabs specialized for adult life in sandy beaches been reported in raven diets.

OBSERVATIONS

On 18 August 2010 at 1350 hrs PST, while walking the ocean side of Netarts Spit at Cape Lookout State Park, Tillamook County, Oregon (45° 25’ N. 123° 58’ W), we encountered a group of three Common Ravens on the sandy beach near the upper edge of the swash zone (the area covered by active wave action); low tide was at 1308 hrs PST. At ~100 m distance with 10X binoculars we could see the ravens, spaced ~20–30 m apart, were hunting for objects buried in the sand. We focused our attention on the nearest raven, since all three appeared to be doing the same thing. During the next 5 min the raven walked a distance of ~25 m just above the upper limit of wave action, and paused to extract items buried in the sand five times, of which four attempts (80%) were successful. The raven was hunting female sand crabs (Emerita analoga), based on their shape (like a pigeon egg) and size (~ 3.5 cm carapace length, or twice the size of males; Efford 1970) in the raven’s bill; we also photographed a gravid female (3.5 cm carapace length) on the beach and examined the last crab attacked by the raven (about the same size). The sand crabs we found during 6 days on Netarts-area beaches were mostly adult females carrying clusters of eggs wrapped under their telsons. Clusters can include 1,000 eggs or more, depending on female size (Efford 1970); clusters we examined were an orange mass half the carapace length.

Upon pausing, the raven made an initial stab into the sand with its bill to a depth of ~3–5 cm, flipped the sand aside, then made 2–3 additional stabs into the sand pit before extracting a crab with its bill. The crab was placed on its back on the sand, held in place with a foot, and then pecked on the ventral surface of it’s body several times before the raven walked away to make a
new attempted capture several meters distant. Apparently, captured crabs were left mostly intact; the one we examined before waves washed it away had the telson removed and no eggs were present. Thus, it appeared the ravens were capturing female sand crabs to eat the egg clusters carried by them; some of the crabs may have been fatally wounded during capture, but none of the captured crabs was eaten.

DISCUSSION

Several aspects of our observation of raven predation on sand crabs are worth noting. First, the ravens must have been using subtle cues to locate the sand crabs, because the crabs were completely buried in the sand, and repeated wave action made the beach surface smooth. Surface movements by crabs to new locations on the beach occur rapidly (in < 10 sec) and only when they are submerged in waves (MacGinitie 1938, Efford 1965), conditions apparently avoided by the ravens. At most, only the small eyestalks and first pair of antennae (used for respiration) project above the sand (Ricketts et al. 1968) and form a small opening in the sand. These small appendages also redirect receding water, leaving a small V-shaped pattern in the sand. Human observers can see both cues, and the ravens may have learned to associate them with the presence of hidden sand crabs.

Second, adult female sand crabs are not uniformly distributed over the beach, but are more abundant lower on the beach than males and are most aggregated on a daily basis during low tides (Ricketts et al. 1968, Perry 1980); peak aggregations occur during two seasons, one of which is in late summer. The conditions under which we made our observations (low tide in mid-August) were particularly favorable for finding female sand crabs.

Third, exploitation by ravens of sand crabs on the northern Oregon coast is a behavior probably learned during the last 20 years. The North American range of Emerita analoga, the only member of the genus found on western U.S. beaches, includes the Pacific Coast from Baja California, Mexico to Kodiak Island, Alaska (Efford 1976); populations inhabiting beaches north of California are patchily distributed and largely dependent on recruitment by zoeal larvae traveling from California as planktonic drift in the Davidson Current (Efford 1970, Sorte et al. 2001). Recruitment of sand crabs on the Oregon coast is particularly successful during El Niño years, but the ability of northern Oregon populations to persist in non-El Niño years is questionable (Sorte et al. 2001). Sand crabs first appeared on northern Oregon beaches in 1992, were noted annually during the next decade (Sorte et al. 2001), and continue to occur there during at least some years.

How ravens learned to exploit female sand crabs for their eggs is not known. Ravens could have discovered that females carry egg masses in autumn by examining injured or dead gravid females stranded on the beach, as we did. Learning where to look for gravid female crabs when they are buried in sand seems initially more challenging. One possible method is by observing and copying the behavior of another predator of sand crabs. Western Gulls (Larus occidentalis) are resident year-round on the Oregon coast, capture and consume a variety of live and dead animal matter that also appear in the diets of ravens, including intertidal invertebrates (Pierotti and Annett 1995), and would seem an ideal species for ravens to copy. We have seen Western Gulls on Netarts Spit capture small invertebrates they stirred up from the wet sands of the swash zone through the process of foot paddling (Hendricks and Hendricks 2006), including earlier on the day we saw the ravens reported here. Western Gulls frequently hunt sand crabs on California beaches in spring and autumn (Smith 2007) and it is possible they do the same along the Oregon coast, although we have yet to see them capture sand crabs on Oregon beaches. Ravens could also have learned to exploit live sand crabs by watching Sanderlings (Calidris alba) and other shorebirds during autumn as they hunt and consume smaller juvenile and male crabs (carapace length typically < 1.5 cm) and the egg clusters of female crabs too large to be eaten whole (MacGinitie 1938, Maron and Myers 1985, Kvitk and Bretz 2005, Smith 2007).

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LITERATURE CITED


Cavity-nesting by the Black-billed Magpie (Pica hudsonia)

K. Richard Stauffer1 and L. Scott Johnson2,3

Abstract.—We describe the first known instance of Black-billed Magpies (Pica hudsonia) nesting in a fully enclosed, pre-formed cavity. Magpies built an undomed nest of sticks in a nest box designed for Wood Ducks (Aix sponsa) near Olds, Alberta, Canada, in 2008. All nesting material was removed from the box after an apparently successful nesting attempt. Magpies built a new nest in the box and fledged at least four young in 2009. These observations indicate that cavity nesting is a distinct, novel behavioral trait that can arise in this species. We describe several potential costs of cavity nesting in this species, which may explain in part why this trait has not become established in any of the many studied magpie populations around the world.

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Species in many avian families nest in pre-formed cavities in trees, rocks, or other substrates. Cavity nesting presumably evolved in lineages in which nesting outside of cavities is ancestral (e.g., Hirundininae, Winkler and Sheldon 1993) when some individuals acted on a propensity to construct at least part of the nest within a pre-existing enclosed space. Cavity nesting then spread in the population because it resulted in relatively high fitness and was also heritable, either genetically or culturally.

Humans are rarely in a position to document the occurrence in nature of a distinctly novel, potentially adaptive behavior trait such as cavity nesting. We provide the first recorded case of Black-billed Magpies (Pica hudsonia) nesting in a fully enclosed, pre-formed cavity.

Background and Observations

Magpies of the genus Pica are permanent residents throughout much of the northern hemi-
sphère and are among the most studied bird species (Birkhead 1991, Trost 1999). Males and females typically work together to construct a large, domed structure made of sticks in a tree or shrub (Erpino 1968, Buitron 1988, Trost 1999). This dome is anchored by a grass-lined mud cup. The dome of sticks over the nest cup presumably decreases predation risk of adults, young, and eggs, especially by owls and larger corvids (Erpino 1968, Baeyens 1981). The dome usually has one, narrow, often difficult to identify entrance.

Our observations were in an area of mixed farmland ~8 km southwest of the town of Olds, Alberta, Canada (51° 45’ N, 114° 14’ W; 1,036 m asl). Magpies are common in this area and typically nest in willow (Salix babbinus) trees, which grow throughout the local area in drainages and other unsuitable locations. KRS frequently observed magpies in late April 2008 near a wooden nest box constructed for Wood Ducks (Aix sponsa). This box had been erected in spring 2006 but had not been used in 2006 and 2007. The box was mounted 4.1 m above ground on a live poplar (Populus spp.) tree, 25 m from open water at the edge of a slough. Magpies had built nests in several locations within 300 m of this tree in previous years although the nests were typically ≤3 m from the ground in willows rather than in other available poplar trees. The box was 60 cm tall and 26.7 cm deep and wide (floor area = 711 cm²). A rectangular entrance hole 11.4 cm wide and 10 cm tall was centered 43.8 cm above the bottom of the box. The box contained a large undamaged nest of twigs topped by a grass-lined mud cup when checked in September 2008. The cup was sufficiently high within the box that an incubating or brooding adult could see out the box entrance hole. The carcass of a fully feathered magpie nestling was in the cup. The cup was soiled with feces suggesting that at least several young had survived late into the nestling stage and probably fledged. All nesting material was removed from the box at this time.

Magpies again used the box in 2009. It seems likely the same pair was involved although this was not confirmed as the adults were unmarked. The nest contained four, possibly five, hatchlings when first checked on 13 May. One young had fledged to the tree near the box and at least three young were visible in the nest entrance on 10 June (http://www.youtube.com/watch?v=153T1xyypM). All nesting material was again removed from the box on 15 August. The box was not used by any species in 2010.

**DISCUSSION**

This is the first report to our knowledge of a magpie using an enclosed, tree-like cavity with a relatively small entrance hole. Holyoak (1967) noted the presence of a nest of a Eurasian Magpie (P. pica) in a "hole" in a cliff on the Calf of Man in southern England, but provided no details on the nature of this hole, i.e., whether it was a true cavity or simply a crevice.

Whether a novel trait increases in frequency within a population depends in part on how that trait affects individual fitness. Use of a cavity for nesting has potential advantages for magpies including greater shelter from precipitation, solar radiation, and wind. The nest would also be better concealed from predators and probably would be more resistant than a typical nest to entry by certain predators, e.g., crows (Corvus spp.) and common raccoons (Procyon lotor). However, cavity nesting would also have several potential costs. Given their size, magpies would require relatively large cavities with large entrance holes, which will be scarcer than other types of cavities. Magpies rarely reuse nests (typically <25% of the time; Trost 1999, see also Antonov and Atanasova 2003), which exacerbates this problem. Magpies potentially could use many of the cavities created by nesting Northern Flickers (Colaptes auratus). Wiebe (2001) reported the mean ± SD diameter of entrance holes to flicker nests in western Canada is 6.42 ± 0.91 cm (n = 143). Measurement of museum specimens suggests that most adult magpies would fit through a hole of this diameter. The mean ± SD maximum diameter of six anatomically complete adults preserved in alcohol was 5.7 ± 0.5 cm (range: 5.1–6.3 cm) whereas that for 9 individuals prepared as stuffed study skins was 6.4 ± 0.3 cm (range: 5.9–6.7 cm). However, after entering a flicker cavity, magpies would be more confined than in a traditional nest. Mean ± SD floor area of 139 flicker cavities examined by Wiebe (2001) was 166 ± 77 cm² whereas data in Silloway (1900) suggests the area of the mud nest cup in a magpie nest is typically about a third larger than the floor area of flicker nests. Magpies using flicker cavities would also be in direct competition for nest sites not only with flickers (which reuse nest cavities) but also other species that use flicker holes, most notably American Kestrels (Falco sparverius), a cavity-nesting raptor. Kestrels would likely dominate
magpies in contests for cavities as, in Europe, Common Kestrels (*F. tinnunculus*) frequently usurp magpie nests for their own nesting attempts (Prokop 2004; see also Becker 1987).

In addition, both male and female magpies have elongated tail feathers that can grow to >30 cm in length. Tails could be prone to damage when entering and moving about in the confines of a cavity. Research in Spain suggests the extent to which a magpie’s tail is damaged signals both age and individual quality and could affect social status and mating success (Blanco and de la Puente 2002). Magpies in Northern Ireland with unbroken and less abraded tails pair earlier and fledged more offspring than magpies with damaged tails; individuals with badly broken tails often remain unmated (Fitzpatrick and Price 1997).

LITERATURE CITED


Botteri's Sparrow (Peucaea botterii) Occurs in Northern Coahuila, Mexico

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ABSTRACT.—Botteri's Sparrow (Peucaea botterii) occurs widely in the shrub-grasslands of southern North America. We report a breeding population of the species in the Sierra de la Encantada of northern Coahuila, Mexico, ~80 km from the Big Bend area of Texas and >300 km from the nearest previously known breeding range in southern Coahuila and central Chihuahua. We captured three individuals, which show a mostly gray dorsal coloration, suggestive of the te.xana subspecies, occurring from southern Texas to northern Veracruz. The exact affinity of the northern Coahuila population still needs to be ascertained. The presence of Botteri's Sparrow in northern Coahuila may have been overlooked previously or may be part of a (temporary) range expansion. More work is needed to map the occurrence of Botteri's Sparrow in northcentral Mexico grasslands.

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Botteri's Sparrow (Peucaea botterii) occurs from southeastern Arizona through western Mexico to Nicaragua and from southern Texas to the Yucatán; the species also breeds in southern Coahuila (Howell and Webb 1995). The authors of the Coahuila State bird list mention Botteri's Sparrow only as a migrant (Garza de León et al. 2007). Occurrence in much of the northern part of the species' range is discontinuous because of fragmentation of natural shrub-grasslands due to overgrazing and agricultural conversion (Ripley 1949, Webb 1985). However, despite expansion of intensive agriculture and ranching (Ceballos et al. 2010), there are still pockets of intact grasslands in northern Mexico that may hold populations of Botteri's Sparrow. Our objective is to describe a previously unknown population in northern Coahuila, Mexico.

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OBSERVATIONS

We surveyed the Valle Colombia ranch in the Sierra de la Encantada of northwestern Coahuila (28°39′7.31″N, 101°20′16.40″W) on 24-26 June 2010. We found several singing male Botteri's Sparrows, as well as young lacking tail feathers, a strong indication of local breeding. The Valle de Colombia area consists of lightly grazed montane (1,350 m) native grasslands interspersed with Prosopis spp. (Fabaceae), Koebelirlia spinosa (Koeberliniaceae), Flosrensia cernua (Asteraceae), Berberis trifoliolata (Berberidaceae), and local stands of Yucca spp. (Agavaceae). Winter shrub cover (x ± SD) varied locally from 1.28 ± 1.12 to 6.68 ± 5.48% (January 2010). Sparrows were most frequently observed singing from the tops of Prosopis spp. We were able to capture three individuals, two males and a female. Birds were dissected to establish gender. Body mass (x ± SD) was 19.8 ± 2.5 g, tarsal length was 20.5 ± 1.6 mm, wing length was 62.0 ± 0.6 mm, tail length was 60.6 ± 0.6 mm, bill length was 10.9 ± 0.4 mm, bill width was 5.8 ± 0.2 mm, and bill height was 5.3 ± 0.1 mm. Dorsal coloration, the most variable character within the species (Webster 1959), was mostly gray with a profusion of rufous streaks. We deposited a sound recording of a male song from the Sierra de la Encantada in xeno-canto (www.xeno-canto.org, accession number XC57103).

DISCUSSION

Botteri's Sparrow occurs rarely in southwestern Texas (Bryan 2002), and breeding of the species in northwestern Coahuila constitutes a northward shift in the central part of the known range of the species by >300 km. Northern Coahuila is poorly sampled ornithologically and our records of Botteri's Sparrow in the Sierra de la Encantada may only represent a fraction of the species' population in the region. Suitable, intact grassland habitat may be present elsewhere in the area, including potentially Texas, only 80 km from the current population. The occurrence of a small, now possibly extinct population in central Chi-
huahua (Meents 1979), may be an indication that Botteri's Sparrow is, at least locally, more widespread in northern Mexico than thought. Alternatively, the lack of earlier records of the species may indicate Botteri's Sparrow occurrence in northern Coahuila is part of a range extension. More work in the region is needed to ascertain whether the Sierra de la Encantada birds represent an isolated population or whether they are part of a discontinuous, but more widespread occurrence in the area.

The dorsal coloration of birds from the Sierra de la Encantada is suggestive of the \textit{texana} subspecies, which ranges from southern Texas to northern Veracruz. The \textit{arizonae} subspecies is distributed from Arizona south to Durango, and presumably includes the central Chihuahuan population. Birds from northern Coahuila may as well belong to the \textit{arizonae} group due to geographical proximity and subtlety in plumage differences between subspecies. It is also possible the Sierra de la Encantada population represents an undescribed subspecies. Morphometrics of our birds provided no information for assigning subspecies: male tail length was within the range of both the \textit{texana} and the \textit{arizonae} subspecies and male wing length was typical for \textit{arizonae} and only slightly smaller than for \textit{texana} (Webster 1959). We know of no known consistent vocal differences between subspecies (Webb and Bock 1996).

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**LITERATURE CITED**


The Orange-breasted Thornbird (Phacellodomus ferrugineigula) (Furnariidae): A New Effective Host of Shiny Cowbird (Molothrus botariensis) (Icteridae)

Giovanni Nachtigall Mauricio1

ABSTRACT.—Over 250 bird species have been listed as victims of the Shiny Cowbird (Molothrus bonariensis), a well-known obligate brood parasite. Five of the nine species of Phacellodomus (thornbirds) have been listed as victims, but none has been reported rearing cowbird fledglings. I report observations of a pair of Orange-breasted Thornbirds (Phacellodomus ferrugineigula) rearing two fledgling Shiny Cowbirds in southern Brazil. These data add a new host for the Shiny Cowbird and constitute the first report of a species of the genus Phacellodomus as an effective host of cowbirds. Received 5 January 2011. Accepted 30 March 2011.

The Shiny Cowbird (Molothrus bonariensis) is a well-known generalist, obligate brood parasite occurring from southern Argentina to the southern USA (Lowther and Post 1999). The list of birds parasitized by this icterid has increased significantly since the early compilation by Friedmann (1929). Whereas Friedmann (1929) found 98 species and subspecies parasitized by the Shiny Cowbird, Lowther and Post (1999) listed 232 species as parasitized while that total reached 251 in the most recent and updated compilation (Lowther 2010). Five of the nine species of the furnariid genus Phacellodomus (thornbirds) have been reported as being parasitized by the Shiny Cowbird (Lowther 2010). Among the remaining four species is the Orange-breasted Thornbird (P. ferrugineigula), an Atlantic Forest endemic recently split from the Orange-eyed Thornbird (P. erythrophtalnus) (Simon et al. 2008). I present the first record of parasitism of the Orange-breasted Thornbird by the Shiny Cowbird, documenting it as an effective host of the cowbird.

OBSERVATIONS

Data on interactions between the Shiny Cowbird and Orange-breasted Thornbird were gathered at the edge of a large peat marsh at the beach town of Laranjal (31° 46' S, 52° 14' W, sea level), municipality of Pelotas, Rio Grande do Sul, Brazil. These observations were made on a daily basis between 2 and 21 December 1997, resulting in 30 hrs of field work (30 min to 5 hrs per day). I discovered a pair of out-of-nest Shiny Cowbirds on 2 December 1997 soliciting food from a pair of Orange-breasted Thornbirds on the edge of the dense vegetation of the marsh bordering the urbanized area of the town. The parasites were in brown (1) and blackish (1) plumage, the latter matching the description of the melanogyna female morph (Fraga in press). On average (± SD), they were fed by their hosts 10.2 (± 3.2) times/hr (range = 8–15), considering only periods of continuous observations of the parasites (n = 4 hrs). All food items observed in detail (n = 26) were insects, of which most were small (smaller than or as large as the thornbird's bill), but at least six were caterpillars larger than bill size and five were dragonflies. The parasite pair generally followed the hosts very closely, soliciting food on most occasions when the thornbirds emerged from the dense marsh vegetation where they routinely foraged. The thornbirds also followed the cowbirds to feed them, in several cases climbing to considerable heights (e.g., 4 m...
in a tree) to deliver food. The blackish plumaged cowbird flew at least 100 m southward at a considerable height on 16 December and was no longer observed. Only the brown plumaged cowbird was then detected and apparently abandoned the territory of the hosts by 21 December, when it flew to the south. No cowbirds were detected following the Orange-breasted Thornbirds in subsequent days.

**DISCUSSION**

A pair of Orange-breasted Thornbirds, supposedly the same reported here, has been monitored in this area for several years, its territory covering a narrow band of ~140 m along the wooded marsh edge (GNM, unpubl. data). However, while provisioning the pair of cowbird fledglings the fumariids extended their territory ~100 m in a perpendicular line from the main axis, crossing a relatively busy road. The Orange-breasted Thornbird is fairly common in the study area, but the above example of parasitism was the only one involving the Shiny Cowbird observed during >15 years of continuous ornithological studies. Another marsh fumariid, the Yellow-chinned Spinetail (*Certhiaxis cinnamomeus*), has been observed feeding young cowbirds in the same area but, in the only reported case, the young parasite died before fledging (Dias and Maurício 1997). The bird species most frequently observed feeding Shiny Cowbird young at the site were Rufous Hornero (*Furnarius rufus*) and House Wren (*Troglodytes aedon*), which apparently constitute usual hosts (GNM, unpubl. data).

It is known that adults other than the hosts may occasionally feed out-of-nest cowbird fledglings and the observation of a certain species feeding cowbird fledglings may not actually designate an effective host (Lowther 2010). However, it is reasonable to assume that the pair of Orange-breasted Thornbirds, which were the only individuals observed feeding the young cowbirds during 20 days, represented the true host, i.e., the birds which received the cowbird eggs and incubated them. The observations reported here show that thornbirds are capable of rearing cowbird fledglings until independence.

It is important in the study of brood parasitism to document species capable of successfully rearing young cowbirds (Lowther 2010). Thus, documentation of fledged young until independence, where the only evidence of parasitism of a certain species is from cowbird eggs or nestlings, is crucial. Other *Phacellodomus* species are not known to have reared cowbird young (Lowther 2010), and the information that the Orange-breasted Thornbird is an effective host is important as it suggests that further studies may document congenerics as effective hosts. It is also important to note that among the 29 fumariid species previously known as victims of the Shiny Cowbird, only five are known as effective hosts (Lowther 2010).

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**LITERATURE CITED**


Ornithological Literature

Robert B. Payne, Book Review Editor

THE EAGLE WATCHERS: OBSERVING AND CONSERVING RAPTORS AROUND THE WORLD. Edited by Ruth E. Tingay and Todd E. Katzner. Cornell University Press, Ithaca, New York, USA. 2010: 256 pages, 14 color photographs, 29 halftones, 1 chart/graph, and 1 table. ISBN: 978-0-8014-4873-7. $29.95 (cloth).—This is a rich collection of creative non-fiction essays from a rather reclusive group of people who are typically limited to publishing purely scientific material: field researchers who study eagles. The editors, Ruth Tingay and Todd Katzner, have at least 30 years of field experience with birds of prey between them and additional experience in the field with other species. Likely through their associations with or positions of leadership in The Peregrine Fund, Hawk Mountain, and the Raptor Research Foundation, they have identified some of the most committed, adventurous, and surprisingly well-written eagle researchers. They also selected an impressive diversity of 24 eagle species including some of the most elusive (Madagascar Serpent Eagle, *Eotriorchis astur,* and New Guinea Harpy [Papuan] Eagle, *Harpyopsis novaeguineae,* and the most highly endangered (Philippine Eagle, *Pithecophaga jefferyi*), as well as the most commonly seen (Golden Eagle, *Aquila chrysaetos,* and Bald Eagle, *Haliaeetus leucocephalus*).

The term "eagle" that unifies the chapters is used in the broadest sense, including birds from several different subfamilies of the Accipitridae: sea eagles, snake eagles, banded eagles, hawk-eagles, harpy eagles. Old World vultures, and sub-buteos. The book opens with a clearly written chapter by the editors on eagle diversity and phylogeny, which serves the purpose of clarifying the now known non-monophyly of "eagles," yet still relies heavily on traditional classification that groups birds with similar ecology, behavior, and morphology (e.g., "Harpy Eagle Group" including Harpy Eagle [*Harpia harpyja*], Crested Eagle [*Morphasis guianensis*], New Guinea Harpy Eagle, and the unrelated Philippine Eagle). The introduction, in addition to eagle diversity, also briefly describes general eagle ecology including diet, foraging behavior, habitat requirements, breeding behavior, and migration. Finally, threats to eagles are addressed, including direct mortality from shooting, trapping, poisoning, and collisions, and indirect mortality from habitat and climate change.

A species description is on the first page of each chapter including common, scientific and other names; IUCN conservation status and population trends; a physical/visual description: physical size; threats; geographic distribution; movements; habitat; diet; and other notes. The need for protection of many of the eagle species is echoed within the chapters as the writers tell of first-hand experience with study birds being shot (e.g., White-bellied Sea Eagle, *Haliaeetus leucogaster,* Chapter 21); habitat destruction, including nesting trees being felled (e.g., Madagascar Serpent Eagle, Chapter 6); and, unexpected assistance (e.g., loggers building a tree blind for study of the Philippine Eagle while felling many neighboring trees, Chapter 25). An appendix charts the IUCN conservation status of all of the world's eagle species (another 51 species for a total of 75), although without the useful added information about population trends in the species descriptions at the beginning of each chapter. Given the conservation focus of the book, appropriately, all royalties are being donated to two leading nonprofit organizations for raptor conservation: Hawk Mountain Sanctuary Intern Program and the National Birds of Prey Trust.

Each chapter, except the Introduction, begins with a species description and is followed by one or more essays written by a researcher with first-hand knowledge of the species as well as a biography of the eagle researcher. Unfortunately, although maybe intentionally, the photographs of the researchers are halftones that leave many of the subjects more obscured than if a photograph had been omitted in the first place. In contrast, the color photographs are as unique and illustrative as the chapters, giving close-up views of the Solitary Eagle (*Harpia harpyja*), Steller's Sea Eagle (*Haliaeetus pelagicus*) and the Eastern Imperial Eagle (*Aquila heliaca*) among others.

It is not clear how the chapter sequence is organized, certainly not phylogenetically or geographically. Some chapters emphasize the utility
and necessity of technology for providing insight into secretive eagle lives (e.g., radio tags on African Crowned Eagles, *Stephanoaetus coronatus*) while others emphasize the important information that can be gained by simple observation with a good pair of binoculars (e.g., Rick Watson on the Bateleur, *Terathopius ecaudatus*). After a few chapters, the repeated translations between metric and English units, in which an originally rough estimate in one unit becomes translated to an absurdly precise one in the other system, become highly irritating. This one annoyance, however, can hardly reduce the significance of the essays as real insider's views to both the lives of and difficulties facing researchers and the eagle species. Chapters range from entirely hilarious (misjudgments regarding a canon net described by Alan Harmata, Chapter 7) to awkward (being the guest of honor at a circumcision ceremony, Chapter 12) to exhilarating near-disasters (being forced to join a weapons-bearing tribal exorcism on the cusp of initiating a violent war, Chapter 2). Befitting the authors' professions as observers in nature, much of the prose is as accurately descriptive as it is beautiful.

Lying against the bark, I tried to catch my breath, clearing mossy dirt from my mouth and feeling the sweat begin to chill against my skin. The first blue hints of daylight drew cautious traces of bird song up through the mists. Dim shapes of trees slowly materialized from the predawn gloom, and beyond them the steep sides of the valley diffused from the sky. The fall of a neighboring tree had torn a great hole in the canopy, allowing me an uninterrupted view of a tangled platform of branches supported by a moss-fringed emergent limb. It was this that had brought me to such a remote corner of the Papuan Eastern Highlands: the nest of a New Guinea Harpy Eagle.

—Martin Gilbert, Chapter 2

For those of us who search out eagle sightings for fun or work, study eagles remotely (i.e., in the laboratory), or just read and dream about them, these chapters give the eagles and those who work with them tangible character. A truly novel idea making for a captivating book, I hope to read more creative non-fiction from some of these authors and others who have dedicated their lives to studying some of the most elusive and captivating species of the world.—HEATHER R. L. LERNER, Smithsonian Fellow. Smithsonian Conservation Biology Institute, Center for Conservation and Evolutionary Genetics, National Zoological Park, P. O. Box 37012, MRC 5513, Washington, D.C. 20013, USA; e-mail: hlerner@gmail.com

RAPTORS OF NEW MEXICO. Edited by Jean-Luc E. Cartron. University of New Mexico Press, Albuquerque, USA, 2010: 710 pages, more than 650 color photographs, 41 color range maps, eight black and white photographs, and 17 figures. ISBN: 978-0-8263-4145-7. $50.00 (hard cover).—Dr. Cartron enlisted 41 other raptor enthusiasts to help write this definitive volume on the diurnal and nocturnal raptors of New Mexico. Jean-Luc Cartron was born and raised in France, where he earned a MD. After traveling the world, he ended up in New Mexico and, for >10 years, has studied raptors and other birds there. He earned a Ph.D. in biology from the University of New Mexico and is now a research associate at that institution.

The stated purpose of this book is to present information from a variety of sources, including publications, reports, field notes, etc., well augmented with photographs, maps, tables, and charts, to fully describe the raptors of New Mexico. This large format tome begins with a Foreword by Rich Gilinski, author of the *Raptors of Arizona*. Following the obligatory preface, acknowledgments, and table of contents are an Introduction and short chapters on raptor morphology (photographs with arrows pointing to the parts of raptors) and species distribution maps. Two introductory chapters discuss the State's floristic zones and vegetation cover, and raptor migration through the State. Both are covered well and in detail, the latter by raptor expert Jeff Smith, which includes many maps showing recoveries of banded raptors, charts and graphs showing timing of migration, and photographs of the raptors themselves.

Next follows the species accounts, the heart of this book, which vary in length from 10 to 26 pages. Each of the 37 species accounts (24 diurnal and 13 nocturnal raptors) is written by one to four coauthors (some by the editor himself) and starts with a full page color photograph of the species. Each account begins with a general description of that species, including plumage, taxonomy, similar species, vocalizations, etc., and continues with sections on distribution, habitat, life history, intraspecific interactions, predation and interspecific interactions, and status and management.

This book was not intended to be a field guide, as that is covered in specialty guides. Some accounts include a short acknowledgment section. All are well illustrated with numerous photographs (most of which have descriptive captions) by 109 different photographers. The photographs vary in size and quality; some are very good, but others are fuzzy or show distant raptors, much as we see them in the field. Accounts of raptors that breed in New Mexico include photographs of breeding habitat, and all include a range map that is color coded for different seasons or with arrows showing migration pathways or both. All range maps show county borders and major rivers. Most accounts include a varying number of tables, graphs, and figures showing prey taken and other interesting information. An extensive bibliography ends each species chapter.

Seven species that have occurred in New Mexico as vagrants are covered in the next chapter; all are shown in one or more photographs. This chapter also includes an extensive bibliography. The book ends with a short concluding chapter, appendices listing egg sets in the Museum of Southwestern Biology, and some data on Flammulated (Otis flammeolus) and Great Horned (Bubo virginianus) owls, and a glossary.

This book sets a high standard for a State raptor book. It meets its stated goal of combining information on raptors in New Mexico from a variety of sources with many color photographs, maps, graphs, charts, and tables resulting in a well written and informative book. It is recommended for all serious raptor enthusiasts, as much of its contents apply beyond the borders of New Mexico. It is a must for Southwestern birders, ornithologists, and raptorphiles.—WILLIAM S. CLARK, 2301 South Whitehouse Circle, Harlingen, TX 78550, USA; e-mail: raptours@earthlink.net

PROCEEDINGS OF THE 4TH INTERNATIONAL PARTNERS IN FLIGHT CONFERENCE, 13–16 February 2008. McAllen, Texas, USA. Edited by T. D. Rich, C. Arizmendi, D. W. Demarest, and C. Thompson. Partners in Flight. 2009: 712 pages, 17 color and numerous black and white figures. Free (Paperback).—This is a hardcopy version of the conference proceedings posted online (www.PartnersInFlight.org). International conferences of Partners in Flight (PIF) are held irregularly as needed. Partners in Flight was organized in 1990 to address long-term population declines of birds breeding in North America and wintering in the Neotropics. Its focus is primarily on landbirds. The theme of the conference reported in this volume is “Tundra to Tropics: Connecting Birds, Habitats, and People”. The papers are divided into nine categories, starting with “Needs Assessment”. Although the Needs Assessment was compiled and written after the conference, it is justifiably the lead section. This section contains three summary papers on Education, Outreach, and Communications Needs; Monitoring Needs; and Research Needs. The remainder of the volume contains 87 papers and expanded abstracts divided among eight categories: Basic Biology; Bird Communities; Anthropogenic Impacts; Decision Support Tools; Education, Communication, and Outreach; Project Implementation; Monitoring; and Response to Habitat Changes. Most of the papers are in English, some are in Spanish and all have Spanish and English abstracts.

There is a heavy emphasis on management, monitoring, and implementation of conservation projects and fewer papers on basic biology compared to similar conferences. Hopefully, this is an indication that avian conservation has grown beyond the learning-about-the-problem phase and is now more focused on developing and implementing conservation projects (as opposed to studies). Another area that received an increase in the number of presentations/papers is monitoring. Most of the papers in this category were focused on monitoring population and community responses to management practices and habitat changes, but monitoring citizens’ perceptions of conservation was also covered.

The most significant section of the volume is the Needs Assessment. Some of the “needs” are idealistic but many are practical, even obvious: for example, distinguishing among education about birds, education about conservation, and education about avian conservation. With the limited resources available for education, research, and conservation, it is important to clearly state the objectives of a funding proposal or conservation effort.

Education, Outreach, and Communications Needs.—The premise is that these needs are essential to achieving conservation success and have not received adequate attention. This paper deals with how to distribute information but
provides little insight on the information to be distributed, other than "conservation". The important point is that we need to do a better job of educating people and the authors propose an increased focus on promoting PIF to other conservation partners. Conservation managers need to identify a specific issue, determine the target audience, the message they want the recipients to learn, and a specific resulting action by members of the audience. Bird conservation education has lagged behind conservation efforts in general and received fewer resources. The resources that been received have often gone to bird education rather than bird conservation education. The procedures and practices that are developed for bird conservation education must be prioritized and should follow the North American Association for Environmental Education Guidelines for Excellence and other accepted standards of best practice. One-third of the needs identified at the conference were focused on the area of Education, Outreach, and Communication. The field needs a defined funding mechanism so that it can advance in an organized fashion.

Monitoring Needs.—Monitoring avian populations is an obvious component of all successful conservation projects. There are ~1,000 avian monitoring programs currently underway in the U.S. This level of effort is admirable but there has been little effort expended to standardize data collection protocols or techniques, or even to share data directly. The document lists eight areas of high priority monitoring needs. Some areas are targeted to fill information gaps (e.g., What is the effect of capturing birds for the cage-bird market on the wild population?), others are to continue ongoing monitoring programs (e.g., How is climate change affecting avian population sizes and distributions?). New techniques and technologies are briefly reviewed and their potential contributions to avian monitoring programs assessed. One of the obvious needs is to standardize the data in GIS format "user-friendly" and "web-based" so that it will be accessible to a greater cadre of users, both scientists and non-scientists. This is the most clearly written and developed of the three "Needs" chapters. The final section on Next Steps enumerates what the authors gleaned from the participants. Some recommendations are essentially to continue along the current paths but others are to develop tools that will enhance the existing data and future data collection. One need is to develop a database of metadata describing the population monitoring data sets.

Research Needs.—This chapter contains a review of many of the previous and ongoing research programs monitoring avian populations, and then identifies knowledge gaps. A high priority to aid in identifying gaps is the development of a database that contains what is known about the demographics and life history characteristics of avian species. A second category of need is to examine the effects of human activity on avian populations; these include activities that can be managed (e.g., habitat modification, ecotourism) and those that cannot (e.g., global warming). The proposed Next Steps include the development of metadata about existing data sets, which are contained in data bases, reports, and publications. This will be an extremely huge undertaking because of the number of resources that exist. The data need to be summarized within a database so they can be analyzed and compared with other studies for identification of knowledge gaps.

These chapters on "Needs" provide an ambitious but necessary road map for avian conservation in the Western Hemisphere; the challenge will be to find the funding necessary to begin working on the individual needs, especially where compilation across multiple data sources is involved.—ROBERT C. BEASON, P. O. Box 737, Sandusky, OH 44871, USA: e-mail: Robert.C.Beason@gmail.com

COMMUNITY ECOLOGY OF TROPICAL BIRDS. By E. A. Jayson and C. Sivaperuman. New India Publishing Agency, New Delhi, India. 2010: 259 + xvi pages, 18 color plates. ISBN: 978-93-80235-16-5. $48.00 (hardback).—Despite the generality of the title, this book reports the authors' own research on bird communities at two famous localities in the south Indian State of Kerala. The first half of the book describes a 5-year investigation into the forest birds of Silent Valley and surroundings, and the second half, 3 years of study of the birds of the Kole wetlands. Each half contains chapters on species observed across seasons and years, density estimates, and some information on feeding ecology; no attempt is made to integrate the two halves. The book contains useful information, but could certainly have used a heavy dose of the editorial sword, e.g., the same tables and descriptions of equations...
are, at times, repeated in different chapters and the grammar often goes astray.

The value of studies such as these must ultimately come from the reliability and repeatability of the results—especially as we would like to be able to evaluate future population changes—and this critically depends on clearly stated methodology. Bird censuses were visual, and perhaps auditory; one feels that censuses in the wetlands have more substance than those in the forests, where, for example (following a tradition in Indian ornithology) leaf warblers (Phylloscopidae) get clearly missed (as the authors acknowledge). Attempts to estimate forest bird densities using line transects come out to ~1,000 birds/km², which the authors slate is comparable to other tropical forest censuses but, in fact, is between 1.5 and 6× lower than figures they present from these other censuses. Methods used to evaluate animal prey are well explained in the wetland study, but not at all in the forest study, and such patchiness is a feature of the book.

However, buried in this book is important information. Some examples follow: (1) There is a remarkable density of waterbirds at Kole (the Little Egret [Egretta garzetta] is listed at a density of 35,000/ha (3.5/nv!), although unfortunately the geographic scale is omitted). (2) More than 20 northern wader species are present in large numbers in the winter, but numbers vary substantially and largely synchronously across years. (3) Some aspects of niche partitioning are presented. Quantitative correlates of fish size with body size of herons, and height of foraging in the forest study are particularly useful.

Silent Valley is famous in Indian conservation, not only for its rich diversity of wildlife, but also because initial work on a dam in the late 1970s, and potential destruction of the valley, was halted as a result of a fledgling environmental movement in India, and then prime minister Indira Ghandi’s environmental awareness (new proposals for a smaller downstream dam are currently being pushed). The two sites studied in and near Silent Valley are “disturbed” areas, and bird species composition reflects this with bulbuls, babblers, and bush-chats recorded as common. It would be of interest to know the composition of more pristine sites, or indeed, if such sites exist. The wetland site, Kole, is largely submerged for 6 months of the year, and much of the area is used for rice production, but land is increasingly being reclaimed and, as in the case of Silent Valley, it is difficult to know the extent to which the study covers more or less human-influenced areas.

The importance of both localities to a developed nation is becoming evident to conservationists, as is the potential short-term economic gain for developers. The authors of this book are commended for the massive amount of data they have collected in the field, and for compiling it through to publication. They note that both Silent Valley and Kole contain south Indian endemics (4 from Silent Valley) and globally near-threatened and vulnerable species (6 are listed from Kole), and in a short section emphasize the threats to the region. More, much more, research can only help conservation of these spectacular places.—TREVOR PRICE, Professor, Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637, USA; e-mail: pricet@uchicago.edu

A BIRDWATCHERS’ GUIDE TO CUBA, JAMAICA, HISPANIOLA, PUERTO RICO & THE CAYMANS. By Guy Kirwan, Arturo Kirkconnell, and Mike Flieg. Illustrated by Tony Disley. Prion Birdwatchers’ Guide Series, Prion Ltd., Cley, UK. 2010: 198 pages with maps and line drawings. ISBN: 978-1-871104-12-7. $41.99 (paper).—This is a detailed bird finding guide to the Greater Antilles plus the Cayman Islands. Puerto Rico and Jamaica are popular venues for formal bird tours and individual birdwatchers. Hispaniola is less well known and, for most U.S. birdwatchers, Cuba has been wishful thinking. The Greater Antilles is rich in regional and island endemics, and offer excellent opportunities for birding. Accommodations are adequate, road conditions are fair to excellent, distances are short, and vehicles are available in most areas for the independent birder. Guided tours on Cuba have burgeoned from Europe and Canada. The chapter on Cuba implies that one could bird Cuba independently as well, although one of the authors, Kirkconnell, is listed as a bird tour guide. The situation regarding the U.S. ban on travel to Cuba is not described; it doesn’t apply to the United Kingdom. U.S. birders interested in Cuba will have to investigate the travel options available, which vary over time.

The Antillean fauna is well known and well-illustrated identification guides exist for the entire region (Raffaele et al. 2003; A Guide to the Birds
of the West Indies) and for individual islands. The book by Kirwan et al., begins with 30 pages of introduction covering travel advice, accommodation, climate and clothing, safety, health and medicine, books, maps, and seasons. Attention is given to keeping costs moderate, but a gratifying feature is that the hook does not dwell on how to find the right bus, hitchhike, or find birds on $5.00 per day. Birding has become expensive and the bright side is that ecotourism may promote conservation. The new Guide emphasizes the species endemic to individual islands or to the Greater Antilles and is directed at bird watchers in general as well as “listers” or “twitchers”.

There is a brief introduction and a map for each island with numbered localities corresponding to sites that are described (but not necessarily in the order in which they appear in the text). Birding localities are listed for Cuba (48 sites including 18 on the Zapata Peninsula), Jamaica (6 sites), Hispaniola (12 sites), Puerto Rico (12 sites), and Caymans (6 sites). There is an introductory paragraph for each locality with the location or directions, site birding strategy, and a list of birds. The latter are often listed as “possibilities”, when it would have been more helpful to have sorted out the “probabilities”, even to the point of percent of trips observed. The text is generally clear and useful, although some sections would benefit from attention to sentence structure and more paragraph breaks.

The most valuable pages for many birders, including this reviewer, concern Cuba which remains terra incognita. The 48 pages provide never-before-seen details on how to see almost all of Cuba’s endemic species. Not having been to Cuba, I cannot comment on the location details, but the lists of accessible endemics elicits salivation. Increasing field experience in the past decade and knowledgeable guides, make it possible to see almost all of them. The Ivory-hilled Woodpecker (Campephilus principalis), however, has not been observed in the past 25 years, despite several intensive searches.

Jamaica and Puerto Rico are much smaller than Cuba. Their avifauna is more familiar, and the endemics on both islands are virtually all accessible on a short trip. The casual birder to Jamaica will miss several species that are believed extinct, such as the endemic petrel and poorwill, which I sought in vain —50 years ago.

I “tested” the Jamaican and Puerto Rican sites where I had personal experience and found the site descriptions clear and lists complete. I cannot comment on the accommodation information (many of them are quite new). However, the directions are clear and, at times, illustrated with maps. The birds listed generally match what I found there. I was amazed that some species, particularly West Indian Whistling Duck (Dendrocygna arborea) are now reported from many localities, indicating a gratifying population increase. Twenty to 40 years ago this was a tough species more often sought in vain than seen. In contrast, in 1972 there was a lookout in Luquillo Forest where one could be confident of seeing wild Puerto Rican Amazon (Amazona vittata) flyhys in the early morning. Ironically, at that time the population was near its nadir of 13 known individuals (1975), whereas it is currently more stable at ~40 birds (2006).

A few pages are devoted to the Caymans, where the main target is a parrot. Jamaica with only six sites (the same number devoted to the Caymans), may seem to get short shrift. However, the nice thing about Jamaica is its relative ease of birding with Hardwar Gap and Windsor Cave, still the most productive sites, yielding a large majority of the island endemics. The 20 pages devoted to Puerto Rico will get birders onto most of the endemics and near endemics. It is particularly gratifying that the best location for the Elfin Woods Warbler (Dendroica angelae) is Maricao Forest, a population that Guy Tudor, David Hill, and I discovered in 1972 in the same month the species was formally described in Auk. This well-marked warbler, discovered in 1968 by Angola Kepler in Luquillo Forest, created quite a stir among the museum “crowd” that was incredulous that such a species could remain undiscovered for so long in such a well-studied avifauna.

Hispaniola is a large island with a large number of endemics and near endemics, but relatively few well-established birding locations, virtually all in the Dominican Republic. A visit to the Sierra de Bahoruco area should produce most of the more elusive endemics, although apparently the road to Aguacate is in no better condition than we found it in 1972. There are several new birding sites, that were not well known 40 years ago, and some of these have official protection. Haiti’s only endemic is the Gray-crowned Tanager (Phaenicophilus poliocephalus), a species one may choose to skip to avoid a depressing and potentially hostile tourist environment. However, the book
describes a trip to the pine forests above Kenscoff where I had the privilege of watching parakeets and crossbills in the same tree.

The selective species accounts (albeit without scientific names) provide a bird finding guide for the species a lister "needs". I would have found it easier to use if it was arranged strategically: Greater Antillean endemics, Multi-island (near) endemics, Island endemics. The full species table (11 pages including scientific names) gives occurrence and status on each of the island groups. A recommendation for a future edition is a list for each of the islands where the endemics and near endemics are listed by location. This would greatly assist individuals with limited time in choosing which one or a few locations would yield the greatest diversity. Astute readers will be able to extract this from the text.

It is gratifying that species names are capitalized, a practice that should be followed by all bird books to avoid confusion in identifying which words are adjectives and which are part of a proper noun (i.e., little Blue Heron vs. Little Blue Heron [Egretta caerulea]). A book that focuses on endemics must be cognizant of taxonomic status and recent splits and lumps. The authors do quite well listing recently split species and acknowledging they are "sometimes treated as subspecies of..." The tenuous and tentative status of some splits is mentioned, for instance under Loggerhead Kingbird (Tyrannus confusiceps). I could not find mention of the basis for English names used anywhere. I was stumped, for example, by the Hispaniolan Highland Tanager and had to check the species list to find this refers to the White-winged Warbler (Xenoligea montana).

A species index would enhance the utility of the guide. My copy of the book was poorly produced as the binding is awkward for the first half where the left hand page trails almost into the gutter. Overall this is a well thought out and well-constructed birding guide to a fascinating and accessible birding region with a high proportion of endemic species.—MICHAEL GOCHFELD, Rutgers University, Piscataway, NJ 08854, USA; e-mail: gochfeld@eohsi.rutgers.edu

BIRDS OF THE MIDDLE EAST. Second Edition. By Richard Porter and Simon Aspinall. Princeton University Press. Princeton, New Jersey, USA. 2010: 384 pages and 176 color plates. ISBN: 978-0-691-14844-1. $39.50 (paperback).—The Middle East is a fascinating zoogeographic region, linking Europe, Asia, and Africa; it therefore has strong influences from the avifauna of each of these regions. Further, some parts of the Middle East show high rates of endemism, especially in the mountain ranges of southern Arabia in Yemen and Saudi Arabia. The first edition of this book, published in 1996, provided the ornithological community with an opportunity to study the region's entire avifauna with all its diversity. Some Middle Eastern endemics depicted in that edition were not shown in any other field guide. Richard Porter was joined by Steen Christensen and Per Shiermacker-Hansen to produce that ground-breaking book. Richard Porter is certainly one of the most knowledgeable ornithologists of this region and, for the second edition, was joined by Simon Aspinall, a UAE-based birder.

Years have passed since the publication of the first edition, and the region has received more and more ornithological attention. Of special note are the first and second editions of The Birds of Europe by Svensson, Mullarney and Zetterstöm that set new standards for regional field guides in detail and accuracy, and which are relevant to most parts of the Middle East. Thus, an update of the first edition of Birds of the Middle East was necessary because of recent advances in the ornithological knowledge of the region. Porter and Aspinall made major improvements by changing the book format to the more user-friendly plate-facing-text format. This has made the book slimmer and compact; it can now easily fit into a trouser pocket rather than be carried inside a bag.

The taxonomic order used in the second edition follows most recent publications and the distribution maps have been completely revised; they now include separate representations for the different seasons. More than 100 species that did not appear in the 1996 edition were added; some are a result of new species discovered in the region, while others resulted from taxonomic changes and advances. Of special note are the large white-headed gulls, which are now treated in great detail. The taxonomic approach adopted by the authors is impressively advanced with Steppe Gull (Larus barabensis) treated as a full species and not as a subspecies of Caspian Gull (L. cachinnans). The advanced treatment of the "small shearwater" complex is also impressive and useful. Some distinctive subspecies are given
more attention compared to the first edition, such as 'Black' kites (Milvus spp.), Daurian and Turkestan shrikes (Lanius spp.), Long-tailed Tits (Aegithalos caudatus), and more. However, some important and distinctive subspecies have been left out, i.e., 'pekinensis' Common Swift (Apus apus), which is widespread in the Middle East on migration, and Oriental Turtle Dove (Streptopelia orientalis) that occurs in the Middle East as a rare visitor. The trade-off of having a slim and compact book is having less space for demonstrating different plumages and variation within species. This is especially evident, which is odd in some cases as many plates have been reorganized which left substantial blank space. For example, on plate 62, Temminck's Stint (Calidris temminckii), a common and widespread species in the Middle East, has only one illustration. An additional illustration could have made an important difference with so much empty space on that plate. There is almost no representation of the birds' habitats in the background of the illustrations. That could have added to the understanding of the ecological requirements of many species. One rather odd split is the Common (Eastern) Nightingale (Luscinia megarhynchos golzi). This form is not normally recognized as a potential split; hafizi is usually used for this eastern taxon rather than golzi, and the illustration is far too dark and rufous. Some plates needed redrawing but were not. Plates 46 (bustards and cranes) and 73–77 (terns) especially look old-fashioned, have little detail, and misrepresent the birds' jizz with short legs and large heads and bills. Many details in the text are given about vagrancy into the region. This is valuable information, but there seem to be many errors in the data presented. Sixteen species recorded in Israel by 2008 are not mentioned as vagrants into Israel, while out-of-date data resources were apparently used which led to incorrect information. For instance, the Plain Leaf Warbler (Phylloscopus neglectus) is mentioned as a vagrant in Israel. This erroneous record originates from older checklists that have been replaced by newer checklists and resources about the birds of Israel (these newer resources even appear in the references chapter). The Black Wheatear (Oenanthe leucura) has been observed in Israel; it does not appear in the main text, but appears in the checklist at the end of the book. Crested Honey Buzzard (Pernis ptilorhynchus) is a scarce migrant and rare winter visitor to Israel, and is a popular target species for visiting birders to Israel. It appears only as a vagrant in this edition. I hope similar errors do not exist for other countries in the region.

This book is invaluable for birders visiting remoter parts of the Middle East, such as Iran, southern Saudi Arabia, and Yemen. The specialties of those parts of the Middle East do not appear in most field guides. Thus, this edition is an essential identification reference for Middle Eastern endemics and specialties, and for many eastern subspecies of common Western Palaearctic species that migrate through or overwinter in the Middle East. It is also an important reference for all birders with a general interest in the avifauna of the region.

This edition is somewhat limited for serving birders visiting more popular regions such as Israel and Turkey. The lack of detail on variation in these countries and different plumages among species, combined with the relatively lower quality level of some of the plates, becomes a disadvantage compared to other field guides. —YOAV PERLMAN, Israel Ornithological Center, Society for the Protection of Israel, 2 Hanegev Street, Tel Aviv 66186, Israel; e-mail: yoav.perlman@gmail.com

CHECKLIST OF THE BIRDS OF NEW ZEALAND, NORFOLK AND MACQUARIE ISLANDS, AND THE ROSS DEPENDENCY, ANTARCTICA. Fourth Edition. By Checklist Committee (OSNZ). Ornithological Society of New Zealand and Te Papa Press, Wellington, New Zealand. 2010: 500 pages. ISBN: 978-1-877385-59-9. NZ $100.00 (soft cover).—The islands of the New Zealand archipelago and the region around the New Zealand base on Ross Island, Antarctica, are true ornithological hotspots. Both enthusiasts and scientists flock to visit New Zealand to spot endemic avian lineages, make natural history discoveries, and test critical behavioral and ecological theories; they also experience and learn from pioneering conservation management to protect a unique avifauna in the face of imminent extinction caused by introduced mammals. For example, New Zealand's birds provide distinct opportunities to study the evolution of flightlessness, cooperative breeding, reversed sexual dimorphism, seabird diversity, host-parasite coevolution, the impact of
climate change on Antarctic food webs, and even the behavioral and sensory ecology of extinct species. Each of these concepts and themes has been featured in classic and recent, high profile general and specialist peer-reviewed articles and popular press highlights, confirming that avian research from New Zealand continues to generate broad impacts on the advance of not only ornithology but biology in general.

Against this background of ornithological discoveries in New Zealand sensu lato, the new edition of its ornithological Checklist provides a much needed comprehensive and up-to-date guide to the taxonomy, distribution, and diversity of extant and extinct avian taxa. A 'checklist' is not the type of book that one reads in one sitting from cover to cover or for aesthetic pleasure and its value becomes evident when it is used for a specific purpose. For example, we write our positive evaluation and enthusiastic recommendation because it is based on fresh experience: our review of the Checklist was completed immediately after having worked on a manuscript concerning the molecular phylogeny of New Zealand's songbirds. We used the Checklist extensively to confirm the New Zealand occurrence of particular species and to obtain the citation of the original scientific description, nomenclature, synonyms, and current classification of all the species included in our analyses. Access to a comprehensively assembled and carefully proofed data base is critically important in systematic, comparative, and species-level research. For example, there remain inconsistencies in applying unique English names for each New Zealand bird species because of overlap with existing English names of birds from other biogeographic regions; to illustrate, the Brown Creeper (Pipipi) (Finschia [Mohoua] novaezeelandiae) of New Zealand is phylogenetically distinct from the Brown Treecreeper (Clinaxteris picumnus) of nearby Australia and the Brown Creeper of North America (Certhia americana).

Regarding local common names, the Checklist also provides an appendix of a valuable and informative list of Maori terms in use for native bird species, but here again many names overlap to include several species or higher taxonomic units. Finally, because of ongoing scientific discoveries, there has been a distinctive flux of the Latin names of the species, genus, and family assignments of Australasian, including New Zealand, bird taxa. The value of the new Checklist is that these sources are compiled, detailed, checked, and referenced.

The Checklist begins with a highly informative introduction to its content, including sections on the treatment of extinct and introduced bird species, and the use of species-specific ektoparasites for identifying avian host taxa. It is then intuitively organized in a top-down fashion, first by taxonomic Subclass, then Order, Suborder, Family, Genus, and finally species and subspecies. A direct synonym system is used to easily distinguish introduced and extinct species. The Checklist does a wonderful job detailing the classification of species within diverse Orders where placements have been historically, and even recently, difficult and complex; notably within the Cuculiformes and Passeriformes. The author members of the Checklist Committee, by their own admission, have been quite careful and conservative in their assignment of taxonomic classifications, to come to a consensus for the placement of all 435 species listed in the book. To the benefit of the reader, the authors provide justification where necessary for the decision of opting for one published classification over another. Indeed, the book is worth picking up just for the history of taxonomic and phylogenetic classification histories alone! For example, the endemic Whitehead (Mohoua albicilla) has been referred to by 15 different Latin names since 1830, when it was originally designated Fringilla albicilla. Similarly, the South Island Rifleman (Acanthisitta chloris chloris) of the endemic New Zealand wren lineage has undergone 16 Latin name alternatives since 1787. Latin names in prior use are fully cited, should the reader have an interest in following a particular species' taxonomic history.

Each species entry provides fully dated (where possible) information on present and historical ranges within the New Zealand bio-political region, including the New Zealand archipelago itself and all of its outlying islands, Macquarie and Norfolk Islands of Australia, and the Ross Dependency in Antarctica. Historical ranges are often presented with evidence inclusive of the fossil record, which we found particularly appealing. The authors also give detailed information regarding year-round, migratory, and breeding ranges. Many details are devoted to the description of New Zealand's diverse and numerous extinct avian taxa with fossil-record evidence and last sightings given, where possible. There are
descriptions of bird species with failed introduction efforts, those with fully established invasive populations, and those with ongoing intensive reintroduction efforts of endangered or threatened populations.

The Checklist Committee of the Ornithological Society of New Zealand provides a generous and user-friendly book documenting the bird species of these unique lands. The product is a detailed, meticulously researched description of the avian species currently, or at one time, known to reside full or part time within the broad definition of New Zealand. By reviewing historical and current taxonomic classifications, ranges, and reintroduction efforts, *The Checklist of the Birds of New Zealand* also offers readers a second-to-none reference and guide. This handsome and versatile book will undoubtedly be of immense use to research ornithologists, conservation scientists, and citizen bird-lovers alike.—ZACHARY AIDALA and MARK E. HAUBER, Department of Psychology, Hunter College, and Biopsychology and Behavioral Neuroscience Program, Graduate Center, City University of New York, 695 Park Avenue, New York, NY 10065, USA; e-mail: mark.hauber@hunter.cuny.edu

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**Editorial Announcements**

**SEARCH FOR EDITOR AND BOOK REVIEW EDITOR**

I have been fortunate to serve as Editor of *The Wilson Journal of Ornithology* from 2007 to the present. Council of the Wilson Ornithological Society elected me to continue through 2012, and I have agreed to continue through that year. That will be 6 years and I indicated it was my intent to step down at the end of 2012. Thus, we are soliciting inquiries from people who have interest in serving as Editor of *The Wilson Journal of Ornithology* starting with Volume 125 (2013). The person selected will be expected to start by 1 July 2012 by organizing their office, receiving manuscripts, and starting them through the review and editorial process. Their first Issue (March 2013) will need to be sent to the printer by 1 December 2012. Most of the manuscripts in that issue will be those that are already in the system. People with interest in serving as Editor should have broad experience in ornithology, a demonstrated track record in scientific writing and publication, editing, and ability to produce products (the Journal) on schedule. Ability to work with authors is a must.

Dr. Robert B. Payne, who has served admirably as Book Review Editor since December 2008, has indicated his desire to step down as soon as a replacement can be found. Thus, those that may be interested in this volunteer position should contact me immediately. The person selected will be expected to receive books from publishers and select reviewers to produce timely reviews. We have been publishing about six Book Reviews in each Issue of the Journal but the number has varied from ~4 to 7 per Issue. There is no stated tenure for this position and frequently Book Review Editors serve at least through the term of one and, at times, several Editors.

Those interested in the Book Review Editor should contact me (sg-wtp@juno.com) immediately. Council of the Wilson Ornithological Society and the Publications Committee will be involved in review of potential candidates and selection of the next Editor of *The Wilson Journal of Ornithology*. All inquiries can be directed to me or Robert C. Beason, President of the Wilson Ornithological Society (Robert.C.Beason@gmail.com).

Clait E. Braun, Editor

*The Wilson Journal of Ornithology*

sg-wtp@juno.com
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Taxa in the revised Maroon-chinned Fruit Dove (Ptilinopus subgularis) complex from Sulawesi (P. subgularis, upper right, P. epia, upper left, and P. mangoliensis, bottom center). P. subgularis is a Wallacean pigeon whose three taxa occur in a longitudinal continuum from Sulawesi in the west to the Sula Islands in the east. We demonstrate that terminal members of the complex differ in song from the geographically intermediate taxon but resemble each other more closely. We combine the new insights on the distribution of vocal trait variation in P. subgularis with Pleistocene earth-historic information to revise species in the complex.
VOCAL TRAIT EVOLUTION IN A GEOGRAPHIC LEAPFROG PATTERN: SPECIATION IN THE MAROON-CHINNED FRUIT DOVE (PTILINOPUS SUBGULARIS) COMPLEX FROM WALLACEA

FRANK E. RHEINDT,1 JAMES A. EATON,2 AND FILIP VERBELEN3

ABSTRACT.—Leapfrog patterns are a peculiar and little-understood phenomenon in which similar populations at either end of a geographic continuum are divided by dissimilar intervening populations. Leapfrog patterns may be important in allopatric speciation. Most documented cases of biological leapfrog patterns refer to morphological traits in passerine birds, and only few have been reported from outside the Andean region. More importantly, the biological basis of leapfrog patterns continues to elude biologists. We document a vocal leapfrog pattern—possibly the second such case documented—in the Maroon-chinned Fruit Dove (Ptilinopus subgularis) complex, adding to the few known examples of leapfrog patterns from outside the Neotropics and in non-passerines. P. subgularis is a Wallacean pigeon whose three taxa occur in a longitudinal continuum from Sulawesi in the west to the Sula Islands in the east. We used discriminant analysis and other statistical methods to demonstrate that terminal members of the complex differ in song from the geographically intermediate taxon but resemble each other more closely. Plumage in P. subgularis does not exhibit the same geographic distribution of variability, a pattern that agrees with the only other study reporting a vocal leapfrog pattern, and supports an earlier hypothesis that leapfrog patterns arise from stochastic phenotypic changes in geographically intermediate taxa. We combine the new insights on the distribution of vocal trait variation in P. subgularis with Pleistocene earth-historic information to revise species in the complex. Received 13 September 2010. Accepted 20 January 2011.

One of the most puzzling phenomena in trait evolution is the geographic leapfrog pattern. This pattern arises when populations from opposing ends of a geographic continuum resemble each other in a particular character and are divided by populations that differ in this trait. Leapfrog patterns were first characterized in birds (Remsen 1984b), the class in which most cases are reported. Leapfrog patterns are distinguished from ring species, which have geographically circular distributions in which terminal forms are phenotypically different and behave as different biological species where they overlap. Several cases of avian ring species were formerly reported, only one of which—the Greenish Warbler (Phylloscopus trochiloides)—has survived genetic scrutiny (e.g., Irwin et al. 2005). Leapfrog patterns continue to be regularly documented (e.g., Remsen 1984a, Remsen and Graves 1995, Maijer and Fjeldså 1997, Hayes 2001, Johnson 2002, Weir et al. 2008, Mauck and Burns 2009, Cadena and Cuervo 2010).
Leapfrog patterns may be an important aspect of allopatric speciation, because some documented cases refer to clades in which the dissimilar central form is no longer thought to exhibit gene flow with either one or both of the terminal forms and has therefore completed speciation. Most of the cases reported, however, refer to complexes in which species limits are still unclear. This suggests leapfrog patterns may be an important factor in differentiation of these birds and merit the close attention of evolutionary biologists. More research is needed before we can be sure of the exact role leapfrog patterns have in diversification of some bird lineages.

Little is known about the causes of leapfrog patterns. Remsen (1984b) hypothesized they are due to stochastic phenotypic changes in geographically intermediate populations that have not yet affected the terminal populations, and presented evidence for why other hypotheses, such as convergent evolution or ancient corridors between terminal populations, are less likely. Modern phylogenetic studies confirm that terminal populations are not generally sister taxa, despite their greater character similarity (Weir et al. 2008, Mauck and Burns 2009, Cadena and Cuervo 2010).

Remsen (1984b) showed that leapfrog patterns are most prevalent in Andean birds, where they occur in about one fifth of all species complexes that fulfill the minimum requirement of being represented by more than three different-looking taxa. Since Remsen (1984b) first recognized the generality of leapfrog patterns, this peculiar mode of character evolution has been carefully documented in about a dozen bird species complexes, the overwhelming majority being from the Andes (e.g., Remsen 1984a, Remsen and Graves 1995, Mayr and Ewald 1997, Hayes 2001, Johnson 2002, Weir et al. 2008, Mauck and Burns 2009, Cadena and Cuervo 2010) and only a few from other tropical and subtropical areas (e.g., Norman et al. 2002). A number of candidates for leapfrog patterns may be present in the Australo-Papuan region (e.g., Mayr and Diamond 2001), but most remain undocumented (see, however, Norman et al. 2002). The reason why the Andes seem to be so conducive to producing this pattern may be a combination of their geographic linearity, great topographic relief, and high species richness (Remsen 1984b).

Most leapfrog patterns have been documented in morphological characters such as plumage traits, but Remsen (1984b) predicted they may occur in behavioral traits, such as vocalizations, as well. However, such cases seem to have gone largely undetected. The only documentation of a vocal leapfrog pattern of which we are aware relates to the Stripe-headed Brush Finch (Arremon torquatus) species complex (Cadena and Cuervo 2010). This brush finch radiation displays a great mosaic of plumage and vocal trait variation along its Andean range with species from the northern and southern end of the distribution having similar simple-structured songs while geographically intervening species sound more complex.

We report a second case of a vocal leapfrog pattern occurring in the Maroon-chinned Fruit Dove (Ptilinopus subgularis), and use the new insights into geographic variation in vocal traits to address species boundaries in the complex. P. subgularis is a little known Wallacean endemic that is divided into three subspecies: (1) epia from Sulawesi, (2) nominate subgularis from the islands of Banggai and Peleng in the Banggai Archipelago, and (3) mangoliensis from the Sula Islands of Taliahu, Seho, and Mangole (Fig. 1; White and Bruce 1986, Baptista et al. 1997, Coates and Bishop 1997, Gibbs et al. 2001). The species inhabits secondary and primary lowland and hill forest, but becomes rare at higher elevations (Coates and Bishop 1997, Gibbs et al. 2001). It has been reported to range to 800 m asl on Sulawesi (Coates and Bishop 1997, Gibbs et al. 2001), to 900 m on Peleng (Rheindt et al. 2010), and to 1,100 m on Taliahu (Rheindt 2010). It seems to be replaced at higher elevations on Sulawesi by the Red-eared Fruit Dove (P. fischeri).

The taxon epia from the Sulawesi mainland is well-known in terms of life-history, but the two small-island taxa (subgularis and mangoliensis) are little known in life and their vocalizations have remained undescribed (Coates and Bishop 1997, Gibbs et al. 2001). Our poor understanding of their field biology is probably at the root of differences in taxonomic classification between original descriptions and current treatments. Quoy and Gaimard (1830) first described the species from Manado (North Sulawesi) as Columba subgularis, but Oberholser (1918) found the latter name to be pre-occupied and replaced it with Leucotroton epia. Meyer and Wiglesworth (1896), before Oberholser’s (1918) name replacement, described a specimen from the Banggai Islands as a new species Ptilopus [sic] subgularis.
explicitly noting that it was closely related to Columba gularis (Quoy and Gaimard 1830) from Sulawesi, but differed in important aspects. Similarly, Rothschild (1898) described the Sula population as a full species under the name Ptilinopus mangoliensis despite being aware that it closely resembled the two taxa from Sulawesi and Banggai. Peters (1937), in his compilation of the world’s birds, included all three taxa under one species and applied the name Ptilinopus subgularis (Meyer and Wiglesworth 1896), which had priority. Peters’s (1937) lumping was conducted without an accompanying rationale and is one of many instances in which he united similar but allopatric taxa into one species. All subsequent authors (e.g., Baptista et al. 1997, Coates and Bishop 1997, Gibbs et al. 2001) followed Peters’s (1937) treatment, and the question of species status for all three taxa has not been revisited.

The objectives of our work are to: (1) document the unknown vocalizations of subgularis and mangoliensis and the vocal leapfrog pattern that characterizes the biocoustic relationship among all three taxa, and (2) combine the new insights on the distribution of vocal trait variation in the Maroon-chinned Fruit Dove with Pleistocene earth-historic information to revise species boundaries in the complex.

METHODS

Vocal Sampling.—The vocalizations of the two undocumented taxa (subgularis and mangoliensis) were recorded during recent visits to the islands of Peleng (e.g., Rheindt et al. 2010) and Taliabu (e.g., Rheindt 2010). We also obtained recordings of epia from our own sound collections and those of colleagues. Details of all 35 recordings, including localities, dates, and names of the recordists, are provided (Appendix). Both analog and digital recordings were converted into WAV format if they were not created in that format. Recordists used different equipment but we consider equipment bias to be negligible. For example, a close visual examination of sonograms showed the level of variability in background noise and slight differences in note shape among recordings from the same recordist are most often equivalent to, and at times even larger than, the variability among recordings from different recordists. This suggests differences in recording quality are more important than equipment differences. We analyzed multiple recordings from several different recordists for each taxon, which should remove any such bias.
Sound Analysis.—Sonograms of vocalizations were prepared and analyzed using Program Syrinx (Version 2.6 h) from John Burt (available at www.syrinxpc.com). Levels of background noise were set to an equal level, otherwise default settings were used. *P. subgularis* is occasionally heard giving low-pitched alarm-type calls, but its vocal repertoire is overwhelmingly restricted to a single song type that consists of a series of ∼5-30 'whoop' notes delivered at a uniform pace (Fig. 2); this is the only vocalization included in our analyses. We measured four vocal parameters in our recordings: (1) number of 'whoop' notes per song, (2) duration of individual 'whoop' notes, (3) song duration, and (4) pace of song delivery ('whoop' notes/sec). We refrained from including frequency parameters in our analysis of geographic variation in the vocalizations because we know they vary strongly and not on a geographic scale, but at an individual level and even within individuals based on song context. We routinely heard single individuals give the same hooting vocalizations at various frequencies in our field observations of Wallacean pigeons and doves, including also the genera *Macropygia* and Turacoena. Two individuals at times, as in *P. s. mangoliensis* on Taliabu (FER, pers. obs.), induce each other into uttering songs at increasingly higher frequencies during a presumed territorial dispute.

Most recordings contained more than one song bout (157 song bouts in 35 recordings; Appendix). We treated recordings rather than song bouts as the sample points of statistical analysis, because song bouts within a recording are presumably strongly autocorrelated, as they are given by the same individual roughly within the same 5-min period. Different recordings are less likely to exhibit autocorrelation, because in each taxon only 33–56% of recordings constituted second or third contributions by the same recordist (Appendix), the remainder having been recorded by different people on different occasions. Even recordings by identical recordists were often identified as having been uttered by different birds (as in recordings by FER and FV, Appendix). Thus, means of all four vocal parameters were computed for each recording, and means and standard deviations were evaluated for each taxon separately (Appendix). A Mann-Whitney U-test was used to assess the significance of inter-taxon vocal differences (α = 0.01) to account for non-conservatism of this test. We also used Isler et al.'s (1998) vocal diagnosability criterion (henceforth the Isler criterion), which is based on two conditions: (1) there must be no overlap between the ranges of measurements between two taxa; and (2) means (μ) and standard deviations (SD) of the taxon with the smaller set of measurements (a) and the taxon with the larger set of measurements
RESULTS

Measurements, including means and standard deviations, of all four vocal parameters varied among taxa (Appendix, Fig. 3). A Mann-Whitney U-test contrasting all four parameters among the three taxa demonstrated significant differences for most comparisons, except for song duration between subgularis and mangoliensis as well as song pace between epia and mangoliensis (Table 1). Thus, songs of all three taxa are distinct in a range of vocal characters. Judged against the Isler criterion, only three of the 12 taxon-parameter comparisons were diagnosable (Table 1), namely number of notes and song pace between epia and subgularis as well as song pace between mangoliensis and subgularis. This result suggests subgularis is vocally more differentiated than the other two taxa are from each other.

A preliminary inspection of recordings indicated there may be within-taxon differentiation of epia songs. Our epia recordings are from two separate regions of Sulawesi (Fig. 1), and we analyzed means and standard deviations of all parameters for geographical regions separately (Table 2). Only song pace was significantly different between North and Central Sulawesi as...
TABLE 1. Inter-taxon comparisons of all four parameters. *P*-values for Mann-Whitney *U*-test are shown numerically, with significant results in bold. Results of Isler et al.'s (1998) diagnosability criterion are given as abbreviations D = diagnosable or ND = not diagnosable. Blank cells provide no inter-taxon comparison.

<table>
<thead>
<tr>
<th>subgularis (n = 9)</th>
<th>epia (n = 12)</th>
<th>mangoliensis (n = 14)</th>
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<tr>
<td>number of 'whoops'</td>
<td></td>
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<tr>
<td>song duration</td>
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<tr>
<td>'whoop' duration</td>
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<td>song pace</td>
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<td>0.13 ± 0.03</td>
<td>0.15 ± 0.03</td>
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<tr>
<td></td>
<td>1.45 ± 0.24</td>
<td>2.69 ± 1.00</td>
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per Mann-Whitney *U*-test, whereas songs were not diagnosable across geographic regions using the Isler criterion. Thus there may be incipient—potentially clinal—vocal differentiation in epia across Sulawesi, but the differences are not as pronounced as towards other taxa.

Discriminant analysis resulted in a canonical function plot that showed subgularis vocalizations clustering together as a spatial agglomeration separate from mangoliensis and epia with the latter two displaying partial spatial overlap (Fig. 4). Cross-validated discriminant analysis predicted 100% of subgularis individuals to be members of that taxon, while only 75% and 86% of epia and mangoliensis, respectively, were predicted to be members of their own taxon on the basis of the four vocal parameters examined.

**DISCUSSION**

Vocal Leapfrog Pattern.—The three taxa of Maroon-chinned Fruit Dove occur in a line from Sulawesi in the west, across the islands of Banggai and Peleng in the Banggai Archipelago in the middle, to Taliabu and Mangole of the Sula Archipelago in the east (Fig. 1). Previous song descriptions of this pigeon were restricted to epia from Sulawesi, which is the most commonly encountered of the three subspecies. We provide the first documentation of the songs of mangoliensis from the Sula Islands and of subgularis from the Banggai Islands, and demonstrate significant vocal differences among all three taxa (Table 1). We also show the terminal taxa on the west (epia) and the east (mangoliensis) are vocally closer to each other than either is to its geographically adjacent neighbor subgularis (Fig. 4; Table 1). The song of subgularis differs from its eastern and western neighbors in its rapid pace and the relatively large number of ‘whoop’ elements within a single song bout (Table 1). Its acoustical impression on the human ear is different from that of the more similar-sounding epia and mangoliensis songs. Omission of song duration as a vocal parameter in our analysis would have accounted for an even stronger diagnosability score for the song of subgularis compared to the other two taxa. This is especially true considering the similarity of song durations between mangoliensis and subgularis is an artefact of the interplay of many ‘whoop’ notes delivered at a high pace (subgularis) versus fewer ‘whoop’ notes delivered at a lower pace (mangoliensis).

The Sulawesi taxon epia has a much larger...
range than the two other taxa, and our vocal material originates from two geographically distant sites on Sulawesi which displayed slight vocal differentiation, consistent with phylogeographic patterns in amphibians and monkeys (Evans et al. 2003a, b; Evans et al. 2008) that exhibit differentiation across the same regional boundaries within Sulawesi. The over-water distance of the North Sulawesi population is much less to *subgularis* on Peleng than to the other *epia* population in Central Sulawesi. Nevertheless, the treatment of both *epia* populations as a single taxon is justified by morphological uniformity and the limited level of vocal differentiation from each other, which was significantly less than from *subgularis*. Wallacean forest birds such as fruit doves have been known to be poor over-water dispersers since Alfred Russel Wallace noted the scarcity of bird colonizations across narrow sea channels characterized by deep sea trenches (e.g., Wallace [1869]: 187–190).

The present characterization of the vocal similarity between *epia* and *mungoliensis* is the first thorough demonstration to our knowledge of a vocal leapfrog pattern in non-passerines, as well as the first vocal leapfrog pattern from outside the Neotropics. Remsen (1984b) hypothesized the Andes may be conducive to producing leapfrog patterns because of their geographic linearity, topographic relief, and high species richness. However, the present case suggests they can occur in an island setting in Wallacea where none of the three Andean factors is as great. Leapfrog patterns, especially vocal ones, may be much more widespread in birds than assumed, and may be frequently overlooked.

**Does Plumage Variability Parallel the Vocal Leapfrog Pattern?**—Plumage differences among the three *P. subgularis* taxa pertain mainly to underpart coloration (Baptista et al. 1997, Coates and Bishop 1997, Gibbs et al. 2001). Plumage of the eastern terminal taxon *mungoliensis* is most conspicuous: the gray color of the underparts and neck of *epia* and *subgularis* is replaced with lime-green (Gibbs et al. 2001; pers. obs.; the labels of the drawings of *mungoliensis* and *epia* in Baptista et al. [1997] are accidentally reversed). Differences between *subgularis* and *epia* are subtler: *epia* is characterized by a conspicuous yellowish-buff breast patch contrasting with the gray
underparts, but this breast patch is less extensive or absent in *subgularis* (Baptista et al. 1997; pers. obs.). The undertail coverts—dark chestnut in the two small-island taxa—are reported to be paler in *epia* (Baptista et al. 1997), but this is not conspicuous in the field (pers. obs., Frontispiece). Thus, plumage variability in this fruit dove complex does not parallel the vocal leapfrog pattern.

There is also no concordance between acoustic similarities of terminal taxa and geographic variability in plumage patterns in Andean brush finches of the *Arrenon torquatus* complex (Cadena and Cuervo 2010). The unlinked nature of character variability in these groups supports Remsen (1984b) that in that leapfrog patterns may be due to stochastic phenotypic changes in geographically intermediate populations that have not affected terminal populations. However, it may also indicate differential selective pressures on various phenotypic traits within the same taxon.

**Speciation and the Evolutionary Origin of the Leapfrog Pattern.**—It is difficult to identify the cause of the vocal leapfrog pattern in *P. subgularis* based only on vocalizations. Phylogenetic data would be useful in establishing relationships among the three taxa and inferring a speciation scenario. Morphological information suggests the Maroon-chinned Fruit Dove is most closely related to *Ptilinopus* species from Sulawesi and the Philippines (*P. marchei, P. merrilli, P. occipitalis, P. fischeri*) and especially to the Black-chinned Fruit Dove (*P. leclancheri*) from the Philippines with which it forms a superspecies (Baptista et al. 1997). Its origin may lie in Sulawesi, and it could have colonized Peleng, Banggai, and the Sula Islands from there. Hall (2002) showed that Peleng, along with the other Banggai Islands and the Sula Archipelago, closely approached Sulawesi only within the last 4 million years.

Colonization, in whichever direction it occurred, must have included overwater dispersal at least between Sulawesi and Peleng, as these two islands have not been connected by land bridges. The straits between Peleng and Sulawesi are only 14 km wide at their narrowest point (Fig. 1), but constitute a deep sea trench of 400–700 m-depth (Becker et al. 2009). Consequently, sea level reductions of up to 130 m during the glacial periods of the past 3 million years were insufficient to connect the two islands (Lambeck and Chappell 2001, Siddall et al. 2003, Bintanja et al. 2005, Thompson and Goldstein 2005, Caputo 2007). The shallowest sea connection between the Banggai and Sula archipelagos is only ~100 m deep (Becker et al. 2009), although the two island groups are ~80 km apart. Narrow land connections between Banggai and Sula must have existed on ~20 occasions for 10,000–50,000 years each within the last 3 million years (Lambeck and Chappell 2001, Siddall et al. 2003, Bintanja et al. 2005, Thompson and Goldstein 2005, Caputo 2007).

*P. s. subgularis* and *mangoliensis* evolved strong vocal and plumage differences despite the repeated presence of glacial land connections. Some of these land connections may have been too low-lying and unstable to provide breeding opportunities for Maroon-chinned Fruit Doves. However, both taxa occur close to sea level and adjacent to mangrove forests (pers. obs.), and we assume the two taxa have repeatedly met during past glacial periods. Vocal and morphological characters of the two species have not amalgamated despite likely hybridization opportunities. A form of character displacement may have occurred during glacial encounters where *mangoliensis* evolved different underpart colors from *subgularis* with the latter presumably exhibiting the ancestral pattern shared with the allopatric *epia*. Vocally, the geographically intermediate taxon *subgularis* probably evolved a much faster song type that radically differs from the presumed ancestral song type uttered by the two terminal taxa.

**Biological Species Status for All Three Taxa.**—The three taxa *epia, subgularis,* and *mangoliensis* were each originally described as separate species (Quoy and Gaimard 1830, Meyer and Wiglesworth 1896, Rothschild 1898, Oberholser 1918). Their current treatment as one species *Ptilinopus subgularis* dates to Peters (1937) at a time when trinomial nomenclature came into widespread use and ornithologists started to lump similar allopatric forms into polypletic species. This taxonomic approach has often been attributed to have happened under the umbrella of Mayr's (1942, 1969) Biological Species Concept (BSC). However, many of these mergers have not been re-examined under a modern BSC premise, which is more stringent concerning diagnosability and monophyly (Johnson et al. 1999).

The question of biological species status for *mangoliensis* and *subgularis* is straightforward because their ranges cannot be considered allo-
patric in light of the paleo-climatic evidence that suggests several mergers—each lasting 10,000–50,000 years—within the last 3 million years (Lambeck and Chappell 2001, Siddall et al. 2003, Bintanja et al. 2005, Thompson and Goldstein 2005, Caputo 2007). The occurrence of considerable gene flow during these repeated periods would have obliterated the vocal and plumage differences between the two taxa. Also, 20,000 years since the last glacial maximum are not sufficient to develop strongly divergent character suites (e.g., Weir and Schluter 2008).

The taxonomic status of *epia* under the BSC is more complicated, since it has not overlapped with *subgularis*. However, vocal differences between *subgularis* and *epia* are as pronounced as between *P. subgularis* and *P. mangoliensis*, indicating the need to consider *epia* as a distinct species as well. Vocal variation within Sulawesi further supports species-level status of *P. epia*. We observed differences in song pace (Table 2) between the two populations of *epia* in Sulawesi. These differences are audible to the human ear as the Central Sulawesi population utters the 'whoop' notes at a slightly slower pace than the North Sulawesi population. Barringer long-distance overwater dispersal over the Maluku Sea, *subgularis* is geographically much closer to the Central Sulawesi population of *epia* than to birds from North Sulawesi. If *epia* and *subgularis* were conspecific and vocally approached each other with decreasing geographic distance, however, we would expect Central Sulawesi populations of *epia* to have a faster song than birds from the north.

We propose the English name Maroon-chinned Fruit Dove should continue to be used for the super-species containing all three taxa, but that new English names should be used for the three individual species to preclude taxonomic confusion. We suggest "Oberholser's Fruit Dove" as a name for *P. epia* from Sulawesi. This name refers to the describer of *epia* and has previously been used for the taxon (Gibbs et al. 2001). We further suggest "Sula Fruit Dove" as a name for *P. mangoliensis* and "Banggai Fruit Dove" as a name for *P. subgularis*.

**ACKNOWLEDGMENTS**

We thank Bas van Balen, Mark van Beirs, Mike Catsis, Pete Davidson, Bram Demeulemeester, Pete Morris, and Dominique Verbelen for providing their recordings.

**LITERATURE CITED**


White, C. M. N. and M. D. Bruce. 1986. The birds of Wallacea (Sulawesi, the Moluccas and Lesser Sunda Islands, Indonesia). BOU Checklist Number 7. British Ornithologists' Union, Peterborough, United Kingdom.
**APPENDIX.** Recordings and their recordists; means for each parameter analyzed.

<table>
<thead>
<tr>
<th>Recording number</th>
<th>Taxon</th>
<th>Recordist</th>
<th>Site</th>
<th>Date</th>
<th>Mean number of 'whoop' notes/song to nearest integer</th>
<th>Mean duration (sec)</th>
<th>Mean 'whoop' notes/sec</th>
<th>Mean song duration (sec)</th>
<th>Mean vocal pace ('whoops'/sec)</th>
<th>Number of songs in recording</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
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<td>D. Verben</td>
<td>Peleng I.</td>
<td>Oct 09</td>
<td>19</td>
<td>0.061</td>
<td>2.391</td>
<td>7.946</td>
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</tr>
<tr>
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</tr>
<tr>
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</tr>
<tr>
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<td>7.898</td>
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<tr>
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<td></td>
<td></td>
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<td>7.34 ± 0.45</td>
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<td>North Sulawesi (exact locality unknown)</td>
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<td></td>
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### APPENDIX. Continued.

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<th>Taxon</th>
<th>Recorder</th>
<th>Site</th>
<th>Date</th>
<th>Mean number of &quot;whoop&quot; notes (rounded to nearest integer)</th>
<th>Mean duration of &quot;whoop&quot; notes (sec)</th>
<th>Mean song duration (sec)</th>
<th>Mean vocal pace (&quot;whoops&quot;/sec)</th>
<th>Number of songs in recording</th>
</tr>
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<td>2.3552</td>
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<td></td>
<td></td>
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<td>11.00 ± 3.90</td>
<td>0.11 ± 0.03</td>
<td>3.44 ± 1.44</td>
<td>3.27 ± 0.22</td>
<td>Total 32</td>
</tr>
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PHYLOGENY AND TAXONOMIC REVIEW OF PHILIPPINE LOWLAND SCOPS OWLS (STRIGIFORMES): PARALLEL DIVERSIFICATION OF HIGHLAND AND LOWLAND CLADES

HECTOR C. MIRANDA JR., ¹, ⁴ DANIEL M. BROOKS, ² AND ROBERT S. KENNEDY ³

ABSTRACT.—We constructed a phylogenetic hypothesis of the pattern of colonization of Philippine scops owls (Otus and Mimizuku). Two mitochondrial genes, ND2 and cytochrome b, were sequenced for 12 samples representing six Philippine endemic taxa: three endemic species, one of which has three endemic subspecies; and one endemic genus. Topology, branch length information, and sequence divergence were used to present the hypothesis for the pattern, direction, and sequence of island colonization events. Philippine scops owls are in two well-supported clades, consistent with at least two independent colonization routes. One route is represented by the montane clade of Otus sunia, O. longirostris, and O. mirus. The other clade is represented by three subspecies of the lowland O. megalotis. The basal position of Mimizuku gurneyi relative to the megalotis clade suggests early colonization of Mindanao. Branch lengths and sequence divergence data are congruent with the morphological differences among the megalotis races. The three races of megalotis differed in 15 of 16 morphological characters. Based on molecular and morphological evidence, we recognize the following Otus megalotis subspecies as full species: Luzon Lowland Scops Owl (O. megalotis), Mindanao Lowland Scops Owl (O. everetti), and Visayan Lowland Scops Owl (O. nigerrum). We also propose reassigning the Giant Scops Owl (Mimizuku gurneyi) to the genus Otus for phyletic consistency.

Archipelagos are interesting places to study phylogeography and evolution because open seas represent potential barriers to gene flow. The construction of robust species phylogenies in island archipelagos provides important insights to rates, patterns, and modes of species diversification (Lovette and Bermingham 1999, Ricklefs and Bermingham 1999, Coyne and Price 2000, Barraclough and Nee 2001, Turelli et al. 2001, Jones and Kennedy 2008a). The Philippine Archipelago, comprising >7,000 islands, has high endemism and some of the most unique avifaunal lineages in the world (Millermeier et al. 1999, Kennedy et al. 2000, Myers et al. 2000, Peterson 2006). The archipelago is relatively recent in geological time (most islands are <35 million years ago, hereafter mya), and the chronology of oceanic island formations from sea floor tectonic events and patterns of coalescence and fragmentation are well documented (Hall 1996, 1998, 2002). These conditions provide investigators unique opportunities to test hypotheses to explain present patterns of species diversification. Recent phylogeographic studies of some vertebrate groups, such as rodents (Steppan et al. 2003, Jansa et al. 2006), thrushes (Jones and Kennedy 2008a, b), and bulbuls (Oliveros and Moyle 2010) have illuminated complex patterns of diversification within the Philippine Islands. We document the altitudinal pattern of colonization and examine the taxonomy of Philippine scops owls (Otus and Mimizuku) using two mitochondrial genes with additional evidence from morphology.

GEOLOGIC HISTORY OF THE PHILIPPINE ARCHIPELAGO

The Tertiary and Quaternary geological history of the Philippine Archipelago has been well documented (Hall 1996, 1998, 2002). Extensive studies have also investigated the role of past episodic sea level fluctuations and climate changes that shaped the configuration of the islands and formation of distinct biogeographic regions (Heaney 1986, 1991, 2000; Heaney and Rickart 1990; Musser and Heaney 1992; Steppan et al. 2003, but see Jones and Kennedy 2008a).

The Philippine Archipelago is considered geologically young with most land emerging from the sea floor <35 mya. The three distinct geological units that emerged and coalesced over the recent past are the Palawan-Mindoro, Greater Luzon, and Greater Mindanao blocks (Fig. 1). The Palawan-Mindoro block was a part of the mainland Southeast Asia continental shelf and broke away 30–35 mya. Palawan emerged about 5 mya and was connected to northern Borneo, but not to other major islands of the Philippine Archipelago. Luzon Island emerged about 30–
35 mya as a group of small islands, southeast of the current location. Extensive volcanism during the last 15 million years shaped the coalescence of islands to form Greater Luzon, Greater Mindanao, including present-day Samar and Leyte, arose about the same time as Luzon. The Greater Negros-Panay block is believed to have emerged as one oceanic island ~2 mya and recently subdivided into the smaller islands including Panay and Negros (Heaney 1986, 1991; Hall 1996, 1998).

One hypothesis to explain the complexity of community structure in tropical archipelagos is the elevational shifts of biomes during glacial...
cycles. The contraction and expansion of biomes during these cycles led to isolation, or aided in colonization as adjacent islands merged. The montane region expanded down along mountain slopes, while lowland dipterocarp forest retracted as average temperature decreased over time. This model predicts the lowland dipterocarp forest, while retracting at the upper elevational boundary of the mountains, would have expanded as well when areas were exposed with descending sea level. Concomitantly, adjacent islands would be closer together, if not coalesced. This process was hypothesized to have acted as ‘species pumps’ in topographically diverse islands such as the Philippines, that accelerated speciation compared to less topographically diverse regions (Steppan et al. 2003). The biome elevational shift hypothesis predicts that species in montane regions of adjacent islands are sister taxa, and lowland species between adjacent islands are sister taxa.

There are two recognized strigid genera within the Philippines, Otus and Mimizuku. There are seven Philippine species of Otus, five of which are small island endemics: Luzon Scops Owl (O. longicollis), Mindoro Scops Owl (O. mindorensis), Mindanao Scops Owl (O. mirus), Philippine Scops Owl (O. megalotis), and Palawan Scops Owl (O. fuliginosus). The remaining two Otus are not restricted to the Philippines: O. mantanamensis on small islands off Borneo and the Sulu Archipelago, and O. elegans in Batanes Islands north of Luzon (Kennedy et al. 2000).

Early classification based on morphology placed Mimizuku gurneyi as a relict of an ancient lineage, and clustered nigrorum and longicollis as races of the widespread O. spilocephalts (Burton 1973). Marshall’s (1978) classification led to species status for O. longicollis, O. mindorensis, and O. mirus. Research based on vocalizations led to more major taxonomic rearrangements with an increase in the number of Asian scops owl species (Roberts and King 1986, Marshall and King 1988, Becking 1994, Lambert and Rasmussen 1998). Earlier systematic works on Philippine scops owls using different mtDNA genes suggested divergence of the lowland/highland clades and noted the relatively high genetic distances among endemic Philippine scops owls (Miranda et al. 1998). Merger of Mimizuku with Otus was also suggested in that paper and elsewhere (Mindell et al. 1997; Miranda et al. 1997, 1998). König and Weick (2008) cited this previous phylogenetic evidence and mentioned the differences in vocalizations among the O. megalotis subspecies, but did not designate the three O. megalotis subspecies as distinct species. Wink et al. (2008, 2009) also supported the invalidity of the genus Mimizuku.

An assessment of genetic structure among the three megalotis subspecies based on larger sampling should clarify their biogeography and taxonomy. For example, the three island blocks of Greater Luzon, Greater Mindanao, and Greater Panay-Negros were separated from each other by narrow straits of ~25 km in width (Steppan et al. 2003). There should be little or no genetic differentiation among subspecies, assuming these straits did not pose a barrier to dispersal. However, if the distinct phenotypic variation observed among the subspecies is congruent with the mtDNA substructure, one can invoke the notion of reproductive isolation due to a geographic barrier (i.e., the open sea).

We used mitochondrial DNA sequences of two genes, NADH dehydrogenase 2 (ND2) and cytochrome b (cyt-b), to address two questions. (1) Does the presence of multiple scops owl species on islands reflect speciation events or do species assemblages result from multiple colonization events? (2) Do the patterns of mtDNA divergences as shown by gene trees and morphological divergences reflect the current taxonomy for the Philippine Scops Owl (O. megalotis)? Resolution of taxonomy to reflect evolutionary divergences has far-reaching implications for studies of conservation and biodiversity (Zink 2004), especially in a biodiversity and conservation hotspot such as the Philippines (Mittermeier et al. 1999, Myers et al. 2000, Sodhi et al. 2004, Peterson 2006).

METHODS

Taxonomic Sampling.—Tissue samples were obtained during the 1991–1993 Philippine Biodiversity Inventory conducted by the Cincinnati Museum Center (CMC) and the Philippine National Museum. We used 12 individuals representing four species of Philippine scops owls: M. gurneyi, O. longicollis, O. mirus, and O. megalotis, which is represented by three subspecies: O. m. megalotis (lowland Luzon), O. m. everetti (lowland Mindanao), and O. m. nigrorum (Panay).

We used sequences of several Old World Otus taxa from neighboring islands to increase taxon sampling and orient colonization patterns of the
Philippine Islands, (Proudfoot et al. 2007, Fuchs et al. 2008) (Table 1). We included published sequences from two representatives of New World ‘Otus’ (Megascops): M. asio and M. hoyi for proximal outgroups. We rooted our trees using the more distantly related Bubo virginianus.

Laboratory Procedures.—Samples used for DNA extraction were from muscle tissue. DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) was used to isolate genomic DNA. We sequenced cytochrome b (cyt-b) and ND2 using primer pairs L14990/H15646, L15517/H16404 for cyt-b, and L5216/H5766, L5758/H6313 for ND2 (Sorenson et al. 1999). A new primer was designed to sequence ND2 for several taxa: LS217 (5’-CTCCATAATCTCAAAATACACATC-3’) for O. m. nigrorum, O. m. megalotis, and O. longicollis. Reaction tubes contained 5.0 µl of 40 mM magnesium chloride, 2.0 µl of dNTP mix (2 mM for each nucleotide), 5.0 µl of 12 mM of primers, and 5.0 µl of Platinum Pfx DNA polymerase enzyme in a 1:30 dilution (Invitrogen, Carlsbad, CA, USA) and 5.0 µl of template DNA. The 550-600 bp fragments were PCR-amplified in 50 µl reaction capillary tubes using Rapidcycler® (Idaho Technologies, Salt Lake City, UT, USA) with the first cycle at 94°C for 15 sec, followed by 35 cycles at 0 sec at 94°C denaturation temperature, 55–58°C annealing temperature at 0 sec, and 50 sec at 70°C extension temperature. Amplified PCR-products were purified using Wizard PCR Preps Purification System (Promega Corporation, Madison, WI, USA). Sequencing was done using an Applied Biosystems 3730 sequencer (Applied Biosystems, Foster City, CA, USA). Sequences were aligned and fragments assembled using GeneiousPro4.0.3 (Biomatters Ltd., Auckland, New Zealand). New sequences were submitted to GenBank with accession numbers JN131475 to JN131498.

Phylogenetic Reconstruction.—Maximum Parsimony (MP) and Maximum Likelihood (ML) analyses used Program PAUP* 4.0b10 (Swofford 2003). A concatenated data set was generated and analyzed. All MP searches used equal weighting, heuristic search options with 1,000 replicates, tree-bisection-reconnection branch-swapping, and random addition of taxa. Clade support for MP and ML trees was obtained with bootstrap values derived from 1,000 replications (Felsenstein 1985). Program MODEST (Posada and Crandall 1998), using Akaike Information Criteria, suggested General Time Reversible (GTR) plus Gamma model as the most appropriate site-specific model of evolution. We performed ML tree searches using the successive approximations method (Huelsenbeck 1998) in PAUP*4.0b10 to obtain the best-fit trees and parameter estimates. Support for particular nodes was obtained using non-parametric bootstrap (Felsenstein 1985) as implemented in PAUP*4b10 with 1,000 fast-addition bootstrap replicates in a likelihood framework.

Bayesian analysis was performed in MRBAYES Version 3.1 using Markov Chain Monte Carlo (MCMC) tree searches (Huelsenbeck and Ronquist 2001). Four independent searches were performed, each with a cold chain and three heated chains run for 400,000 generations with trees sampled every 100 generations.

Morphometric Analysis.—Specimens (Table 2) from the Delaware Museum of Natural History (DMNH) and CMC were examined at the Houston Museum of Natural Science. Only adult specimens of known gender were included, as specimens of unknown age or gender could bias the results by over- or under-representing mean measurements. Twenty-one specimens (11 males and 10 females) of megalotis, 18 of everetti (10 males, 8 females), and seven nigrorum (4 males, 3 females) were included (Table 2). Culmen (cere to tip) and tarsus measurements were taken with Vernier calipers, and a ruler was used to measure natural wing chord and tail length (all measurements in mm) (Table 2).

Significance of morphometric variation was assessed using ANOVA for differences between megalotis and everetti, whereas non-parametric Mann-Whitney U-tests were used for comparisons of everetti and nigrorum, as only small samples were available for the latter form. Differences were examined separately for males and females in light of variation between male and female owls (Amadon 1959, Brooks and Arnold 2005).

RESULTS

DNA Sequence Analysis.—All samples were sequenced from frozen tissue. We obtained 1,033 and 1,054 bp of ND2 and cyt-b, respectively. We truncated the first 15 bp at the 5’ end of the downloaded sequences because of ambiguous alignment in that short segment. No other insertion or deletion was observed from that point upstream. Alignments were relatively straightforward and were performed by the GeneiousAlign option within Geneious Pro 4.0.3 (Biomatters...
<table>
<thead>
<tr>
<th>Species</th>
<th>Voucher (Field number)</th>
<th>Geographic location</th>
<th>Cyt.b</th>
<th>Source</th>
<th>ND2</th>
<th>Source</th>
</tr>
</thead>
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<tr>
<td>Bubo virginianus</td>
<td>MVZ 18014</td>
<td>USA</td>
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<td>Wink and Heidrich 1999</td>
<td>EU601050</td>
<td>Fuchs et al. 2008</td>
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<tr>
<td>Mimus gurneyi</td>
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<td>Mindanao, Philippines</td>
<td>JN131488</td>
<td>This study</td>
<td>JN131476</td>
<td>This study</td>
</tr>
<tr>
<td>Megascops asio</td>
<td>MVZ 17928</td>
<td>USA</td>
<td>DQ190845</td>
<td>Proudfoot et al. 2007</td>
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<td>Fuchs et al. 2008</td>
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<td>Otus hayi</td>
<td>ZMUC 114834</td>
<td>Bolivia</td>
<td>EU601103</td>
<td>Fuchs et al. 2008</td>
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<td>O. lempii</td>
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<td>EU601112</td>
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<td>Fuchs et al. 2008</td>
<td>EU601033</td>
<td>Fuchs et al. 2008</td>
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<td>O. leptocephalus</td>
<td>UWBM 75379</td>
<td>Russia</td>
<td>EU601111</td>
<td>Fuchs et al. 2008</td>
<td>EU601035</td>
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<td>O. megalotis everetti</td>
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<td>Mindanao, Philippines</td>
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<td>This study</td>
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<td>O. megalotis</td>
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<td>Luzon, Philippines</td>
<td>EU601118</td>
<td>Fuchs et al. 2008</td>
<td>EU601042</td>
<td>Fuchs et al. 2008</td>
</tr>
<tr>
<td>O. basiliscus</td>
<td>UWBM 67567511</td>
<td>Captive</td>
<td>EU601110</td>
<td>Fuchs et al. 2008</td>
<td>EU601034</td>
<td>Fuchs et al. 2008</td>
</tr>
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<td>O. megalotis nigrorum</td>
<td>CMC B40325/(B629)</td>
<td>Panay, Philippines</td>
<td>JN131497</td>
<td>This study</td>
<td>JN131485</td>
<td>This study</td>
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<td>O. mirus</td>
<td>CMC B38100/(B1480)</td>
<td>Mindanao, Philippines</td>
<td>JN131494</td>
<td>This study</td>
<td>JN131482</td>
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<tr>
<td>O. mirus</td>
<td>FMNH 357429</td>
<td>Mindanao, Philippines</td>
<td>EU601126</td>
<td>Fuchs et al. 2008</td>
<td>EU601057</td>
<td>Fuchs et al. 2008</td>
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<tr>
<td>O. spilocephalus</td>
<td>MNHN 15-58</td>
<td>China</td>
<td>EU601116</td>
<td>Fuchs et al. 2008</td>
<td>EU601040</td>
<td>Fuchs et al. 2008</td>
</tr>
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<td>O. suria</td>
<td>MNHN 6-98</td>
<td>Thailand</td>
<td>EU61117</td>
<td>Fuchs et al. 2008</td>
<td>EU601041</td>
<td>Fuchs et al. 2008</td>
</tr>
</tbody>
</table>
The Philippine lowland scops owls appear to be monophyletic with *O. megalotis* and *O. everetti* from Luzon forming a sister clade, and *O. nigromegali* of Panay/Negros positioned basal to the two other races. A subclade within the lowland *Otus* assemblage included *O. bakka- meo*, *O. kempi*, and *O. lettia*. The second major clade comprised montane forms of *O. longicornis*, *O. mirus*, and the non-Philippine endemic *O. sunia*. Within the Philippine montane clade, *O. longicornis* of Luzon and *O. mirus* of Mindanao formed a strongly-supported clade with *O. sunia*. The Indo-Malayan *O. sunia* formed a clade together with *O. insularis*, *O. capnodes*, and *O. moheliensis* of the Comoro Islands and Madagascar (Fuchs et al. 2008). The Mindoro Scops Owl (*O. mindorensis*) was not represented in our study but was previously found to be embedded within this clade (Mindell et al. 1997, Miranda et al. 1999). Except for the *O. longicornis* clade, and the *Otus lettia*/*Mimizuku* gurneyi branch, most basal nodes were strongly supported in MP and ML with 100% bootstrap, and by 1.0 posterior probability in Bayesian analysis (Fig. 2).

Pairwise Sequence Divergence.—The uncorrected-p sequence divergence distances showed significant differences among the three clades: (1) the Philippine lowland endemic *Otus* (including *Mimizuku*), (2) the non-Philippine lowland *Otus*, and (3) the montane clade (Table 3). We selected the nearest-neighbor values as a conservative measure of distance in view of the small sample size used in this study. Pairwise estimates of
FIG. 2. Phylogenetic hypothesis of relationships of Philippine scops owls using Bayesian and Maximum Likelihood (-ln = 10523.52) methods for mitochondrial cyt-b and ND2 genes. The Maximum Parsimony tree is similar except for the position of *Otus lettia ussuriensis*, which is basal to *Mimizuku* and *Otus megalotis*. Numbers above the diagonal represent bootstrap support and numbers below are Bayesian posterior probability support values.

TABLE 3. Pair-wise distances of nearest-neighbor values among terminal *Otus* taxa in each of the three clades based on uncorrected p-distance and Kimura 2-parameter distance (K2P).

<table>
<thead>
<tr>
<th>Clade</th>
<th>Uncorrected p</th>
<th>K2P</th>
<th>Divergence dates (mya)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Philippine lowland clade</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. nigrorum/M. gurneyi</em></td>
<td>0.053</td>
<td>0.056</td>
<td>2.65-2.8</td>
</tr>
<tr>
<td><em>O. nigrorum/O. m. everetti</em></td>
<td>0.036</td>
<td>0.038</td>
<td>1.8-1.9</td>
</tr>
<tr>
<td><em>O. nigrorum/O. m. megalotis</em></td>
<td>0.042</td>
<td>0.044</td>
<td>2.1-2.2</td>
</tr>
<tr>
<td><em>O. m. everetti/M. gurneyi</em></td>
<td>0.058</td>
<td>0.060</td>
<td>2.9-3.0</td>
</tr>
<tr>
<td><em>O. m. everetti/O. m. megalotis</em></td>
<td>0.038</td>
<td>0.040</td>
<td>1.9-2.0</td>
</tr>
<tr>
<td><em>O. m. megalotis/M. gurneyi</em></td>
<td>0.059</td>
<td>0.063</td>
<td>2.95-3.15</td>
</tr>
<tr>
<td>Non-Philippine lowland clade</td>
<td>0.003</td>
<td>0.003</td>
<td>0.15</td>
</tr>
<tr>
<td><em>O. bakkamoena/O. lempiji</em></td>
<td>0.010</td>
<td>0.011</td>
<td>0.5-0.55</td>
</tr>
<tr>
<td><em>O. lempiji/O. lettia</em></td>
<td>0.012</td>
<td>0.012</td>
<td>0.6</td>
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<tr>
<td>Montane clade</td>
<td></td>
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<tr>
<td><em>O. longicornis/O. mirus</em></td>
<td>0.038</td>
<td>0.038</td>
<td>1.9</td>
</tr>
<tr>
<td><em>O. longicornis/O. sunia</em></td>
<td>0.058</td>
<td>0.062</td>
<td>2.9-3.1</td>
</tr>
<tr>
<td><em>O. mirus/O. sunia</em></td>
<td>0.065</td>
<td>0.068</td>
<td>3.25-3.4</td>
</tr>
</tbody>
</table>

* Estimated divergence dates based on the putative 2% sequence divergence per million years calibration (Lovette 2004). The ranges represent the differences between the two models of molecular change (uncorrected p-distance vs. K2P).
FIG. 3. Plots of comparison of morphological characters for *O. megalotis*, *O. everetti*, and *O. nigrorum*: (A) wing vs. tail length for males, (B) culmen vs. tarsus length for males, (C) wing vs. tail length for females, and (D) culmen vs. tarsus length for females.
FIG. 3. Continued.
percent divergence were based on uncorrected-p and Kimura 2-parameter. The average distance within the endemic lowland clade between subspecies of O. megalotis including Minizuku gurneyi ranged from 3.6 to 5.8% (Table 3). The pairwise sequence divergences within the lowland non-Philippine endemics clade (O. hakkanae, O. lempii, and O. lettia) were much lower at 0.03–1.2%, and were comparable to the divergence distance values among the montane clade taxa, which ranged from 3.8 to 6.5%.

Our preliminary divergence dating attempts using Beast Version 1.4.8 (Drummond and Rambaut 2007) suggested the first invasion of the archipelago started in Mindanao by M. gurneyi which branched off from the Indian Scops Owl group from the mainland (4.6 mya, 95% HPD = 2.6–5.8). Dispersal to the Greater Panay Island block may have occurred after emergence of the landmass (2.4 mya, 95% HPD = 1.7–3.3), followed soon after by dispersal back to Mindanao and to Luzon (2.2 mya, 95% HPD = 1.4–3.1). The montane invasion of the islands started at about the same time (2.5 mya, 95% HPD = 1.2–3.7).

Morphometric Variation.—Specimens of megalotis were significantly larger than everetti, which were significantly larger than nigrorum (Table 2). All 16 tests were significant except tail length was not significantly different between everetti and nigrorum (Fig. 3). Measurements of male megalotis were significantly greater than everetti for wing (F = 29.28, P < 0.0001), tail (F = 8.08, P < 0.01), culmen (F = 8.21, P < 0.01), and tarsus (F = 48.47, P < 0.0001). Female megalotis were also significantly larger than everetti for wing (F = 26.80, P < 0.0001), tail (F = 13.12, P < 0.002), culmen (F = 46.78, P < 0.0001), and tarsus (F = 24.68, P < 0.0001). Measurements of male everetti were significantly larger than nigrorum for wing (Z = 2.82, P < 0.001), culmen (Z = 1.91, P < 0.02), and tarsus (Z = 1.62, P < 0.05), but not tail (Z = 1.55, P < 0.07). The same pattern held for female everetti, which were significantly greater than nigrorum for wing (Z = 2.04, P < 0.02), culmen (Z = 2.16, P < 0.01), and tarsus (Z = 1.59, P < 0.05), but not tail (Z = 0.91, P < 0.18).

Contrary to the typical reversed sexual size dimorphism (RSD) found in owls, only one of the 16 measurements showed a larger character for males than for females. Male nigrorum have longer tarsus length than females (Table 2), but this should be interpreted with caution due to the limited sample size.

Plumage Variation.—We focused on diagnostic differences among the three taxa. The taxon megalotis has two characters the other two lacked; scapular stripes and tarsal feathers extending onto the upper part of the foot. A reddish-colored head characterizes nigrorum in contrast to megalotis and everetti.

The darkest taxon is everetti, which has dark brown underparts and is nearly black on the nape. In contrast, nigrorum is the lightest taxon with white-striated underparts and reddish nape. Intermediate is megalotis with ashy-brown underparts and brownish nape.

A red morph is also found in megalotis. Two of 21 (10%) specimens examined were red morph (one each from Luzon and neighboring Polillo, both females [DMNH 2816, 14477]), and three (14%) appeared to be intermediates (from Luzon, 2 females [DMNH 52949, 52951] and 1 male [CMNH 38249]).

DISCUSSION

We found that scops owls colonized the Philippines in at least two independent events with subsequent diversification occurring independently in both montane and lowland clades. This pattern is similar to that observed among endemic mammals, although time scales were different (Heaney 1986, 1991; Steppan et al. 2003).

There are three prediction models that explain patterns of colonization in islands with montane and lowland biomes, including: (1) a montane clade nested within a lowland clade on the same island is predicted when a single colonization event of the lowland biome is followed by a cladogenetic colonization by a new population of the montane biome. (2) a lowland clade nested within a montane clade within an island is predicted when a single colonization event of the montane biome is followed by a cladogenetic colonization by a new population, and (3) a separate montane and lowland clade is predicted during multiple parallel colonization events. During the latter, the lowland taxa between adjacent islands should form a monophyletic group while the montane taxa form a parallel clade. The first and second models suggest a cladogenetic speciation event within an island. The third model suggests independent parallel altitudinal colonization events. Cases supporting all three hypotheses have been reported in New World avian taxa (Rice et al. 1999).
Our study supported the third model. All montane Otus taxa between islands comprised one clade and the lowland Otus in other islands formed another parallel clade. This split within the Otus clade may extend deeper within the strigiform phylogeny: the extent of which can be revealed by more extensive taxon sampling and phylogenetic analysis.

The O. megalotis intraspecific genetic distances was relatively large with p-distance between O. m. everetti and O. m. megalotis at 3.8%, O. m. nigrorum and O. m. everetti at 3.6%, and O. m. nigrorum and O. m. megalotis at 4.2% (Table 3). These values were much higher than the p-distances between the three non-Philippine species with O. bakkamoena and O. lempiji at 0.03%, between O. bakkamoena and O. lettia at 1.0%, and between O. lempiji and O. lettia at 1.2%. The p-distance values observed among the Philippine O. megalotis subspecies were also comparatively higher than those observed between subspecies of other Otus species elsewhere (Prumfield et al. 2007). Genetic distances are approximations of differentiation (Meier et al. 2006) and may not necessarily be diagnostic of species limits (Winkler 2009, 2010). However, the distances we observed are consistent and comparable with species-level differentiation among birds (Kerr et al. 2007). These distances are congruent with the discrete morphological differences among the Otus taxa that we documented in this study.

Estimating divergence dates within a clade based on either island emergence chronology (Cooper and Penny 1997, Steppan et al. 2003, Weir and Schluter 2004) or sequence divergence values (Lovette 2005) are promising but with caveats (Garcia-Moreno 2004). A recent analysis supported the 2% per million years constant of the mitochondrial molecular clock for most avian lineages (Weir and Schluter 2008), and we applied this generality with caution. Our well-supported phylogeny showed the lowland invasion of the Philippine Archipelago by the lineage that led to M. garnesi started in Greater Mindanao. Sequence divergence between M. garnesi and non-Philippine lowland scops owls (O. spiloecephalus/O. lettia/O. lempiji/O. bakkamoena) was calculated at 11 ± 0.06%. Assuming a 2% sequence divergence per million years (at least for the cyt-b gene), a divergence date of 5.5 mya coincided with the most recent date of emergence of Mindanao Island (estimated at 8 to 6 mya). Extensive volcanism followed island emergence from the sea floor, and it is likely that colonization by ancestral M. garnesi occurred much later, rather than earlier. The second calibration was the divergence of O. m. nigrorum from the ancestral M. garnesi. Sequence divergence of 5.6% suggests a colonization date of the Greater Panay-Negros Island block at 2.8 mya. The Panay-Negros block emerged from the sea floor de novo about 2 mya (Steppan et al. 2003); the discrepancy of 0.8 mya can be explained either by (1) later estimates for the emergence of the Panay Negros block, or (2) overestimation of rates due to genetic drift, hollenecks, and founder effects (Carson and Templeton 1984, Thorpe et al. 1994) as the Greater Panay-Negros block experienced fragmentation during the last Pleistocene ice age, 100,000 to 10,000 years ago (Heaney 1986).

We present evidence that parallel multiple colonization in two elevational zones shaped the pattern of the genus Otus community within the Philippine Archipelago. It is possible that Mindanao Island was colonized three times; once along the montane route (O. nitrus), and possibly twice via the lowland route. O. megalotis nigrorum from the Visayas is basal to the much larger Luzon and Mindanao islands. The question for Mimizuku remains whether it represents a lineage from a third colonization event, or speciated de novo within the ancestral megalotis.

Taxonomic Changes.—We reviewed the literature to find the rationale for keeping the three Otus megalotis island populations within one species (Marshall 1978, Amadon and Bull 1988). However, previous phenotypic analysis was lacking and no defined character analysis, based on either morphology or vocalizations, was conducted. Our analyses based on genetic (molecular) and morphological approaches, suggest the three megalotis subspecies represent evolutionarily distinct taxa under the phylogenetic species concept (PSC). We strongly suggest recognition of species status for the three megalotis subspecies; Luzon Lowland Scops Owl (O. megalotis), Mindanao Scops Owl (O. everetti), and Visayan Scops Owl (O. nigrorum). The relatively large size of the Giant Scops Owl represents an autapomorphy but its phylogenetic position as a terminal lineage does not warrant genus status. We suggest the Giant Scops Owl be designated as Otus garnesi.

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**LITERATURE CITED**


SPECIES RANK OF PHIBALURA (FLAVIROSTRIS) BOLIVIANA BASED ON PLUMAGE, SOFT PART COLOR, VOCALIZATIONS, AND SEASONAL MOVEMENTS

A. BENNET HENNESSEY

ABSTRACT.—The Swallow-tailed Cotinga (Phibalura flavirostris) has traditionally been considered to consist of two subspecies. P. f. flavirostris of southeastern Brazil's foothill forest and, isolated by ~2,500 km, a population of P. f. boliviana in central-western Bolivia. The plumage of the two taxa is distinctly different; boliviana males have a longer tail, and body plumage is significantly less sexually dimorphic. The iris of boliviana is mustard yellow, distinct from the blood red iris of flavirostris. P. f. boliviana has dull to bright orange-yellow feet whereas flavirostris has pink feet. Only one vocalization type is recorded for P. f. flavirostris, whereas at least five calls and a song are known for P. f. boliviana, which vocalizes significantly more often. The Brazilian P. f. flavirostris has strong seasonal movements, whereas P. f. boliviana has no seasonal movements. Given the diagnosable differences between the two taxa, it is highly probable they are separate lineages. P. boliviana qualifies as critically endangered for its declining small population due to continued habitat loss.

METHODS

Plumage comparisons are based on 3 boliviana specimens (American Museum of Natural History [AMNH]; Zoological Museum, University of Copenhagen), photographs of 17 individuals (Bromfield et al. 2004; J. C. Atienza, pers. comm.; Mileniusz Spanowicz, pers. comm.) and field observations of 46 boliviana individuals in the Apolo Region (14° 36' S, 68° 30' W) of Bolivia. Behavioral and ecological comparisons are based on a year-round breeding survey (2008) and a continued monitoring program by William Ferrufino, and tape recordings of 13 individuals made during field work on 4, 5, and 18 October 2002, and 4–12 December 2003 in Apolo, La Paz. The flavirostris comparisons are based on eight specimens (AMNH; Philadelphia Academy of Natural Science; Goeldi Museum), 18 hrs of field observations of 14 individuals, and sound recordings of eight individuals from 26 October to 2 November 2004 in Intervales National Park, State of Sao Paolo, Brazil (24° 12' S to 24° 32' S, 48° 03' W to 48° 32' W).

RESULTS

Plumage.—The plumage of boliviana is sexually dimorphic. The male has a dark gray crown with a large, semi-concealed fiery-red central crown patch (central crown feathers tipped black). A well-defined black facial mask bordered by white below and on the neck extends to the ear coverts: it has an orange-yellow malar stripe, chin, and lower throat with some dusky barring laterally; and the sides of neck and breast black and variable white to yellowish-white (upper
breast) or pale yellow (lower breast). The lower underparts are variable yellow, pale yellow (including vent) with slight black streaking on belly becoming denser on flanks; the feathers of the back and rump are brownish-olive with black subterminal bar and contrasting broad yellow tips. The tail is strongly forked, outer feathers rather pointed, outer rectrices black with dusky-brown base, remaining rectrices black with mostly olive-yellow outer and dusky-brown inner webs at base. The wing has blue-black coverts, primaries, and secondaries with the outer webs edged greenish-yellow-olive. The female plumage has more variable streaking, possibly related to age. This similar, but slightly duller overall to the male plumage, dull brown-gray shade of the male’s black mask with black appearing on ear coverts, underparts more extensively barred black (variable), tail notably shorter, outer rectrices dusky-brown with blackish-brown tip, remaining rectrices with mostly olive-yellow outer webs, blackish tips and dusky-brown inner webs; marginal wing coverts at wing bend blackish, remaining lesser and median coverts appear variable from black to dark olive-green tipped black, greater secondary coverts and tertials gray-brown broadly edged greenish-olive on outer webs, and black greater primary coverts.

The most quantifiable characteristic distinguishing the two taxa is the tail length of the males. The only male *boliviana* specimen has a tail length of 131 mm (Chapman 1930; Peter Capainolo, pers. comm.), which is 24.8 mm longer than the mean 106.2 mm (range = 99 to 125.8 mm) tail length of male *flavirostris* specimens (n = 21) (AMNH: Peter Capainolo, unpul. data; Alex Jahn, pers. comm.; Goeldi Museum). There was no overlap in tail length with the longest *flavirostris* tail 5.2 mm shorter than the only adult male tail of *boliviana*. Field observations and photographic comparisons (n = 7) confirm that male *boliviana* consistently have a long tail similar in length to that of the male specimen (pers. obs.; J. C. Atienza, pers. comm.; Geoff Bromfield, pers. comm.; Mileniusz Spanowicz, pers. comm.; Geoff Bromfield, pers. comm.; Mileniusz Spanowicz, pers. comm.).

The extent of barring on female *Phibalura* is variable among individuals, but *flavirostris* is more extensively barred than *boliviana*. The chin and underbelly barring of *flavirostris* is variable in intensity but no individuals show a complete lack of barring (AMNH; n = 21), in contrast with *boliviana* where most females show no barring on the chin or underbelly (n = 32; pers. obs.; J. C. Atienza, pers. comm.; Geoff Bromfield, pers. comm.; Mileniusz Spanowicz, pers. comm.). Female *flavirostris* have dull green upperwing coverts in contrast with the black male upperwing coverts. This feature does not appear to be constant in *boliviana* where, in some breeding pairs, the female has black upperwing coverts. Other than the shorter tail, some female individuals of *boliviana* have plumage features similar to the male, whereas the sexually dimorphic body plumage of *flavirostris* is clearly demarcated in all specimens (n = 12).

The marked differences in female plumage between the two taxa are important in considering why *boliviana* was initially considered only a subspecies. Chapman (1930) in identifying the subspecies status of *boliviana* (based on a single female specimen) did not indicate the *boliviana* female was substantially different from the female *flavirostris*. Chapman (1930) noted there were “marked differences” but concluded this called into question the correctness of the identification of gender. Chapman speculated that it was possible the female *boliviana* used to base his subspecies conclusion “may be a young male”. Snow (1982) agreed the 1902 AMNH female *boliviana* specimen was probably incorrectly assigned to gender. Krabbe (1984) examined all three *boliviana* specimens and compared them with *flavirostris* specimens, and also concluded, based on its distinctively different markings, the single female *boliviana* specimen was incorrectly assigned to a gender. These authorities believed it better resembled a male *flavirostris*, as they were not aware of the different female *boliviana* plumage.

**Soft Part Colors.**—The iris color of *boliviana* and *flavirostris* is distinctly different with no observed variation in color (*boliviana* n = 17, *flavirostris* n = 10, pers. obs.; J. C. Atienza, pers. comm.; Geoff Bromfield, pers. comm.; Mileniusz Spanowicz, pers. comm.). The iris of *boliviana* is mustard yellow, whereas the *flavirostris* iris is blood red. The iris in both taxa is semi-concealed suggesting the color may be involved in signaling.

Foot coloration also differs markedly between the two taxa. Feet of *boliviana* are dull to bright orange-yellow, whereas *flavirostris* feet are dull to bright pink. No overlap has been recorded. Soft part colors were not known for *boliviana* or noted in Chapman’s (1930) classification.

**Vocalizations.**—No vocalizations of *flavirostris* were recorded before this study. I obtained 34
sound recordings (representing at least 8 individuals) of *flavirostris* in Brazil during a similar stage of nesting conditions to compare to recordings of 13 *boliviana* individuals (#'s 120831, 120833, and 120834, Macaulay Library of Natural Sounds, Cornell University, Ithaca, NY, USA). The *flavirostris* vocalizations consisted of a single call note type with only a slight change of form but not frequency (Fig. 1). This call was most often recorded when one individual of a perched pair would call once before flight. No other sound was heard or recorded. The *flavirostris* population is considered to vocalize infrequently (Snow et al. 2004). I heard individuals vocalize on average once every 15 min.

Vocalizations of *boliviana* are highly variable and frequently emitted. One individual gave on average 80 type C call notes per minute over a 4-min sound recording (Fig. 2). Call C is the most common call note, used as a contact call in large flocks perched and in flight. There is also high variation in calling patterns with call types A, B, and C (Fig. 3) repeated without pattern but with slight variation in frequency for long periods. Calls D and E were recorded only once by different individuals (Fig. 3). Several calls can be frequently heard at the same time while *boliviana* forages gregariously; where other call types have been heard but not recorded, Song A shows the only repeated patterned calls recorded for *boliviana* suggesting a song type (Fig. 4). This pattern was repeated without pause for >2 min. A female, while nesting, emitted Call C frequently while alone with a single egg. Single individuals of *flavirostris* while brooding eggs have not been heard to vocalize.

**Seasonal Movements.**—*P. f. flavirostris* has strong seasonal movements from 400 to 1,200 m elevation in Brazil (Sick 1993). Individuals arrive in open foothill areas to breed from October to January. Individuals are entirely absent from these breeding areas for 7 months of the year with unclear movements although some have been observed to move to lowland forest (Snow 1982, Sick 1993). In contrast, *P. f. boliviana* are present throughout the year (1,400–2,000 m asl) where studied and are known to breed from August to March with a peak around January (William Ferrufino, unpubl. data). No seasonal movements are apparent for *boliviana*.

![FIG. 1. Selected call notes of *Phibalura flavirostris flavirostris* demonstrating range of variability, Intervales State Park, São Paulo, Brazil.](image1)

![FIG. 2. Segment of call C sequence of *Phibalura flavirostris boliviana*, Pata, Madidi National Park, La Paz, Bolivia.](image2)
DISCUSSION

Data collection in Bolivia has been intensive in the Madidi Region (Remsen and Traylor 1989, Hennessey and Gomez 2003, Hennessey et al. 2003), and we now know that boliviana is a reproductively isolated population. Given the extreme range disjunction between the two allopatric taxa, it is likely to retain its genetic and phenotypic integrity. From the consistent, diagnosable differences in morphometric plumage, soft part, vocalization, and reproductive seasonal movement differences between the two taxa, it is highly probable these are separate lineages, each on its own evolutionary trajectory. A male boliviana was observed in an exaggerated flight display over two females in December 2003, similar to the flight display observed of Chestnut-crested Cotinga (Ampelion rufaxilla) (Hennessy 2004) where the tail was extended outward. The increased tail length of boliviana as compared to flavirostris, a sexually selected secondary character in its exaggerated form, would appear to demonstrate evolved reproductive behavior changes, possibly involving flight display and mate choice. The much more complex and increased vocal repertoire of boliviana also suggests evolved behavioral differences. The
evolution of less sexually dimorphic traits in *boliviana* suggests a complex change in reproductive behavior and that the two taxa are likely behaviorally reproductively isolated. I propose the local Quechua name, which means fork-tail, as the English name Palkachupa Cotinga for *Phibalura boliviana*, an endemic species for Bolivia.

**CONSERVATION IMPLICATIONS**

The Swallow-tailed Cotinga is considered near threatened (IUCN 2010) and a high research priority (Parker et al. 1996). Its threatened status was based only on known information for *flavirostris*. I estimate, based on field observations, that 400 to 500 *boliviana* individuals are within a broken ring of fragmented habitat surrounding the town of Apolo (William Ferrufino, unpubl. data). Given the habitat destruction in the Apolo area in the last 100 years, *boliviana* qualifies as critically endangered (1b2c) under IUCN criteria for its declining small population due to continual habitat loss. Endangered status is supported by its small range and small population. Much of this range continues to be deforested and burned for cattle pasture and agricultural areas within Madidi National Park’s area of Integrated Management. The largest population is outside of Madidi National Park, around the original collection site of Aten.

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**LITERATURE CITED**


ABSTRACT.—Many authors do not recognize the highland Andean Ibis (Theristicus branickii) as a species distinct from lowland Black-faced Ibis (T. melanopis). We considered this problem using a new system of quantitative criteria for species recognition. Andean Ibis differs from Black-faced Ibis markedly in proportions (shorter bill: mean 118 vs. 140 mm; longer tail: mean 215 vs. 185 mm), structure (no wattle), and color pattern (rufous-chestnut crown, face and nape rather than rufous-chestnut crown only; larger white vs. smaller rusty-buff belly-patch). We propose elevation of Andean Ibis to full species. It is rare in Ecuador and Bolivia, vagrant in Chile and only likely to be moderately abundant in Peru.

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from *caudatus* also apply, namely that the sides of the head are concolorous with the crown, and, in their Latin diagnosis, that the bill is shorter. These points were repeated in English by Salvadori (1900), in an elaborate defense of species status for *branickii* which evidently became lost in time, and by Hellmayr and Conover (1948).

The question of whether *Theristicus branickii* is a species is clearly tied to the question of its morphological distinctiveness. We sought to answer the latter through study of museum specimens, and answer the former by use of a new system for classifying taxa as species or subspecies based on phenotypic differences, which are allocated a score reflecting their perceived magnitude (Tobias et al. 2010).

**METHODS**

We examined and measured adult specimens of *melanopis* (31; 12 males, 11 females, 8 unsexed) and *branickii* (32; 15 males, 9 females, 8 unsexed) to ascertain the accuracy of the original description and resolve the taxonomic status of *branickii*, conclusively, in the American Museum of Natural History, New York (AMNH), Natural History Museum, Tring, UK (NHM), Museum National d’Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Washington, D.C. (USNM), and Zoologisches Museum Berlin (ZMB), and examined photographs of both taxa widely available online. Measurements taken (by NJC), using callipers and rulers, were: length of bill to skin on top of the culmen, tarsus length from top of the tarsometatarsal bone at the rear to the junction with the middle toe at the front, curved wing length from carpal bend to wing-tip, and tail length from tip to the point of insertion. Differences between the two taxa in plumage color and pattern were judged qualitatively by eye except the width of the upper belly-patch, which was measured to the nearest 5 mm.

Tobias et al. (2010) introduced a quantitative system for measuring phenotypic differences between lower taxa based on four categories of distinctiveness, each with a simple numerical score for both morphometric and plumage characters: minor (score 1), medium (2), major (3), and exceptional (4). The scores for the two greatest uncorrelated morphometric differences and three strongest plumage differences are summed, and taxa are treated as species if their overall score reaches seven. Tobias et al. (2010) recommended use of Cohen’s $d$ statistics to quantify effect sizes to discriminate thresholds of morphometric distinctiveness; we used an online calculator (http://www.uccs.edu/~faculty/lbecker/) for these values. The scoring of plumage differences involves an assessment of characters which, although more qualitative because dependent on individual judgment, requires observance of an explicit set of criteria relating to shade, color, contrast and extent, and which thus "minimizes subjectivity and maximizes repeatability" (Tobias et al. 2010:733). However, these criteria do not mention how to score the presence or absence of a feature like a wattle; we equated it to the "presence of an entirely different pattern", which Tobias et al. (2010:733) indicate as a major difference.

**RESULTS**

We found the mensural differences striking (Table 1). The bill of *branickii* is generally much shorter, the legs somewhat shorter, the wing-length longer (there is considerable overlap), and the tail notably longer. There was little overlap in bill or leg length in our sample, and only the slightest overlap (the same value, scored once each) in tail length. We also observed, based on skins and photographs, although not measurable, that the neck of *branickii* appears distinctly shorter than in *melanopis*.

Some seasonal change in the intensity of the rich rufous-chestnut on the face of *branickii* is apparent, and also in the intensity of the buffy-rufous of the neck. Certain features, however, are consistent in all specimens and photographs:

1. *branickii* has the rufous-chestnut of the crown continuing smudgily onto the face and back to a broad area of the upper neck; *melanopis* shows a clear, clean division between the (generally rather paler) rufous-chestnut crown and the lower face, the dividing line running behind the eye and tapering onto the nape (rather than spreading over the upper neck) (medium difference: score 2);

2. *branickii* shows short lines of bare black skin on the submoustachial and malar area and a fully feathered chin and throat; *melanopis* possesses a black semi-circular mesial chin wattle (major difference: 3);

3. *branickii* has a white belly-patch between the gray breast-line and the black underbelly, while the equivalent in *melanopis* is rusty-
TABLE 1. Measurements (mm), Cohen’s $d$ effect sizes and phenotypic difference scores of Theristicus melanopis and $T. \text{branickii}$ specimens at AMNH, MNHN, NHM, USNM, and ZMB. Initials “bpw” = belly-patch width, measured as the distance from the lower edge of the gray breast-band to the upper edge of the black under-belly (to the nearest 5 mm).

| Character | melanopis | | branickii | | | Cohen’s $d$ | Score |
|-----------|-----------| |-----------| | |-----------| |
| Bill | $139.6 \pm 7.3$ | 126-154 | $118.4 \pm 8.0$ | 105-130 | 2.169 | 2 |
| | $79.2 \pm 3.7$ | 72-86 | $69.0 \pm 3.9$ | 60-75 | 32 | 2.706 | 2 |
| Wing | $375.2 \pm 14.9$ | 351-416 | $391.0 \pm 10.9$ | 369-409 | 32 | 1.209 | 1 |
| Tail | $185.2 \pm 9.4$ | 155-200 | $215.4 \pm 9.9$ | 200-238 | 31 | -3.112 | 2 |
| Bpw | $71.8 \pm 20.9$ | 25-105 | $140.4 \pm 19.5$ | 110-180 | 24 | -3.389 | 2 |

Other characters mentioned in the literature for $T. \text{branickii}$, rufous-tinged neck-base, paler foreneck and breast (both perhaps seasonal differences), rather dark gray (or at any rate darker) wing-coverts (there is a trend, but some $T. \text{melanopis}$ are as gray), and grayer upperparts, do not find clear endorsement in the material we have consulted. The differences between the two forms are considerable. Summing the two greatest morphometric differences (tail length, 1; and bill length, 2; Table 1) and the three strongest plumage differences, we have a combined score of 11 between the two taxa. These differences are, following Tobias et al. (2010), more than sufficient to recognize the two taxa as separate species. $T. \text{branickii}$ can actually make a stronger claim for specific status, than $T. \text{melanopis}$ can from $T. \text{caudatus}$, as it more distinct in terms of number of differing characters, given that separation of the latter two species is based (so far as we are aware) on presence or absence of a wattle (score 3) and the former’s all-black belly (3) and white wings (1).

**DISCUSSION**

*Theristicus branickii* is clearly a species rather than a subspecies, based on multiple plumage and morphometric characters. However, Tobias et al. (2010) also considered the option of scoring real differences in behavior and or ecology between taxa. We note that $T. \text{branickii}$ is a bird of upland puna (3,700-4,500 m; Schulenberg et al. 2007), whereas $T. \text{melanopis}$ ranges from sea-level to 3,000 m (Matheu and del Hoyo 1992). The completeness of this elevational disjunction is not known, but we speculate the morphometric disjunctions in the two taxa (notably the shorter bill and legs) are related to differences in foraging substrate that are in turn related to elevation. We also note that, from maps and information in Matheu and del Hoyo (1992) and Delaney and Scott (2006), $T. \text{branickii}$ is resident while $T. \text{melanopis}$ undertakes considerable seasonal migrations.

Puna habitat occupied by *Theristicus branickii* occurs in Ecuador (Antisana, Cotopaxi), Peru (Junín, Huanacavíla, Ayacucho, Cuzco, Puno), northwest Bolivia (La Paz), and extreme northern Chile (Arica) (Steinbacher 1979). The species range-map for *Theristicus melanopis* in Ridgely et al. (2003) suggests an extent of occurrence $>500,000 \text{ km}^2$ for $T. \text{branickii}$, and the combined area of the three Central Andean puna ecoregions is $>480,000 \text{ km}^2$ (World Wildlife Fund 2010), far above the threshold ($< 20,000 \text{ km}^2$; IUCN 2001) for possible listing of the species as threatened on the IUCN Red List.

The species has been described as “uncommon and very local throughout [its] range” (Matheu and del Hoyo 1992: 499), and as “apparently declining in some areas” (Stotz et al. 1996:141). The evidence in Bolivia and Chile strongly suggests numbers cannot have been high. Bolivia seems to be listed on the basis of a single bird taken at ‘Lagonillas’ in La Paz (or now Cochabamba: Paynter 1992) in July 1901 (Chubb 1919; specimen BMNH 1902.3.13.1651). Chile is listed on the basis of a specimen taken in June 1853 in the Cordillera de Arica, where local people once knew it (Goodall et al. 1951) but no longer do so, resulting in the view that the form is accidental in the country (Martínez Piña and González Cifuentes 2004). In Ecuador it has been assumed that numbers were “apparently always very
limited” (Ridgely and Greenfield 2001:142), but specimen BMNH 1920.10.31.5, collected in September 1919 at Lake Mica in Antisana, has a label inscribed “Formerly very abundant but now rather scarce”. Today it is “rare and very local”, with probably fewer than 100 individuals, and “rather wary, doubtless in part because in many areas it is still hunted” (Ridgely and Greenfield 2001:142). It is “widespread but uncommon” in Peru (Schalenberg et al. 2007:80), and it is this country which evidently now holds the key to the long-term survival of the species. It is hard to speculate on the size of the population in Peru, but with so much habitat apparently available we might expect numbers to be in four or five figures.

Delany and Scott (2006), while half-recognizing *Theristicus branickii* as a species, ventured no estimate of its population size.

**CONSERVATION IMPLICATIONS**

*Theristicus branickii* and its upland habitat have several threats. The species is hunted in places (Ridgely and Greenfield 2001), and livestock have degraded vegetation and eroded soils in its puna habitat in Peru and Bolivia with mining activities now causing pollution (World Wildlife Fund 2010). *Theristicus melanopis* has an estimated generation length of 9.6 years (BirdLife International, unpubl. data). Assuming *branickii* is similarly long-lived, these threats have probably produced a population decline over the past three generations (the period used to assess population trends in the Red List criteria: IUCN 2001), i.e., the past 30 years. However, whether the decline rate approaches the threshold for listing as threatened (>30%) is unclear.

A thorough assessment of the species’s conservation status is clearly warranted.

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**LITERATURE CITED**


SONG DIFFERENCES AMONG SUBSPECIES OF YELLOW-EYED JUNCOS (JUNCO PHAEONOTUS)

NATHAN D. PIEPLOW¹,² AND CLINTON D. FRANCIS²,³

ABSTRACT.—We compared 13 song features among three populations of Yellow-eyed Junco (Junco phaeonotus): J. p. bairdi from Baja California Sur, Mexico; J. p. palliatus from southeast Arizona, USA; and J. p. phaeonotus from Oaxaca, Mexico. Songs of J. p. bairdi differed significantly from those of J. p. palliatus in 11 of 13 features and differed significantly from those of J. p. phaeonotus in six of 13 features. Songs of J. p. palliatus differed significantly from those of J. p. phaeonotus in only four of 13 features. Discriminant function analysis clearly distinguished songs of J. p. bairdi from those of the two other subspecies, which were not clearly distinguishable from one another. Additional investigations using playback experiments and genetic analyses may be warranted to better evaluate the merits of promoting J. p. bairdi to species status. Received 22 August 2010. Accepted 24 January 2011.

Ornithologists have long hypothesized that geographic song variation affects gene flow and can lead to assortative mating, reproductive isolation, and population divergence (Grant and Grant 1996, Irwin et al. 2001, Slabbekoorn and Smith 2002). However, the relative extent to which geographic variation in bird song influences speciation remains controversial (Baker and Cunningham 1985, Slabbekoorn and Smith 2002). There are now several recent examples of song variation functioning as a reproductively isolating barrier among co-occurring cryptic species (e.g., Irwin et al. 2001, Toews and Irwin 2008), suggesting song variation may also act as a barrier to hybridization among populations that are currently separated, were they to become sympatric in the future.

The Yellow-eyed Junco (Junco phaeonotus) is a sedentary resident of arid conifer and pine (Pinus)-oak (Quercus) forests with a current distribution restricted to mountains between southeastern Arizona, USA and Guatemala (Sullivan 1999). Geographic song variation in the Yellow-eyed Junco is obvious to the ear and is one factor contributing to disagreement about how many species are involved in the complex. The fifth edition of the American Ornithologists' Union Checklist (AOU 1957) recognized two species; Baird's Junco (currently J. p. bairdi), isolated in the mountains of Baja California Sur, Mexico; and Yellow-eyed Junco (J. p. palliatus) and J. p. phaeonotus), occurring in mainland Mexico and Arizona, USA. The AOU (1957) did not mention J. p. fulvescens or J. p. alticola, which occur in the mountains of Chiapas, Mexico and Guatemala, respectively. The 32nd AOU checklist supplement (AOU 1973) lumped Baird's Junco into Yellow-eyed Junco (J. phaeonotus, including J. p. fulvescens and J. p. alticola) without explaining the rationale for the change, although it cited authors who had lumped the groups (Paynter 1970) or recommended doing so (Mayr 1942). The AOU continues to treat all juncos with yellow eyes as a single species (AOU 1998). Howell and Webb (1995), however, recognized J. p. bairdi as a separate species from the rest of the Yellow-eyed Junco complex.

Howell and Webb (1995) describe marked differences in song between J. p. bairdi and mainland birds: J. p. phaeonotus sings "a varied series of bright chips, often with trills or buzzes thrown in, typically the last note rising or upslurred... [that] can be confused with songs of Rufous-sided Towhee [Pipilo spp.] and Bewick's Wren [Thryomanes bewickii] (page 731), while J. p. bairdi sings "a pleasant, tinkling, and trilled warble... [that] may suggest a small Troglodytes wren and strikingly different from mainland Yellow-eyed Juncos" (page 730). Differences between the songs of mainland J. p. phaeonotus and peninsular J. p. bairdi may be obvious to the human ear, and contributed to Howell and Webb's (1995) treatment of the populations as separate species, but the distinction has not been investigated quantitatively. The objective of this study was to investigate the extent and nature of vocal differences between J. p. bairdi Yellow-eyed Juncos and mainland Yellow-eyed Juncos from two regions (Arizona, Arizona).
USA and Oaxaca, Mexico). This study represents an initial quantitative assessment of differences between these taxa to identify potential barriers to gene flow between the isolated populations and to examine if re-evaluation of the taxonomic status of *J. p. bairdi* may be warranted.

**METHODS**

**Recordings.**—Songs of *J. p. bairdi* were recorded on a Western Field Ornithologists and Sonoran Joint Venture expedition to the Sierra La Laguna, Baja California Sur, Mexico, during 14–19 July 2008. Songs of *J. p. palliatus* were recorded in the Huachuca and Chiricahua mountains, Arizona in May 2009. We considered the difference in the month of recording unlikely to influence study results, as both study sites were visited during the lengthy active breeding season; Arizona Yellow-eyed Juncos raise up to three broods per year from late April to the beginning of August (Sullivan 1999), while juncos in Baja California during the 2008 expedition were at all stages of breeding from nest-building to independent young (Carol Beardmore et al., unpubl. data).

Recordings were made in 24-bit WAV format with a sample rate of 44.1 kHz on a Fostex FR2-LE recorder with a 55-cm Telinga parabola and stereo DAT microphone. Additional recordings of *J. p. bairdi* from Baja California Sur, *J. p. palliatus* from Arizona, and nominate *J. p. phaeonotus* from Oaxaca were assembled from the collections of the Macaulay Library at the Cornell Laboratory of Ornithology, the Florida Museum of Natural History, the Borror Laboratory of Bioacoustics, the Xeno-Canto online collection, and the private collections of S. N. G. Howell, Andrew Spencer, and Richard Webster, as well as the commercially published audio collection of Boesman (2006). Recordings from the Macaulay Library, the Borror Laboratory of Bioacoustics, Xeno-Canto, and Boesman (2006) were originally obtained in MP3 format and converted to WAV format at 44.1 kHz for analysis. Recordings by S. N. G. Howell were digitized in WAV format at 44.1 kHz from the original cassette tape by NDP. Typical songs from each region are illustrated in Fig. 1.

We randomly selected five songs of the same song type from each recording for each individual sampled. The recording contained a single song type in almost all cases; if a recording included more than one song type, we randomly selected five songs of the song type that was most common on the recording. We used Marler and Isaac’s (1961) definitions of junco song features: a note is a continuous vocal utterance, a syllable is two or more notes grouped to form a single coherent unit, a trill is a syllable repeated at least twice consecutively, and a phrase is one or more dissimilar syllables that are separated from other phrases by a trill. We measured 13 song features (Fig. 2): song length (sec), total number of
FIG. 2. Annotated spectrogram of a single Yellow-eyed Junco song from Arizona, USA, illustrating the measurements used in song analysis: (a) song length (sec), (b) two repeats of first unique syllable/trilled unit and its three unique notes (b1–3), (c) four repeats of the second unique syllable/trilled unit and its three unique notes (c1–3), (d) peak frequency, (e) highest frequency, (f) lowest frequency, and (g) frequency bandwidth. This song has six syllables, two of which are unique, resulting in a song average of three repeats per syllable. In this particular example, the number of unique syllables is the same as the number of unique syllables and the number of repeats per trill is three, just as per syllable. This particular song does not have any phrases. Figure 1D, F, G–I illustrate sample phrases (continuous utterances of unrepeated, dissimilar syllables).

syllables, number of unique syllables, mean number of repetitions per syllable, number of trills, mean number of repeated syllables per trill, number of unique notes per trill, number of phrases, mean of number of notes per phrase, peak frequency (frequency of the maximum amplitude), lowest frequency, highest frequency, and bandwidth (highest frequency minus lowest frequency). We calculated the mean for each song feature for each vocalizing individual, and a single mean value represented each variable for an individual bird. All song measurements were performed manually in RavenPro 1.3 (Charif et al. 2008) using a Hamming window and a fast Fourier transformation (FFT) length of 1,024, providing a spectral resolution of 43 Hz.

Statistical Analyses.—We used two complementary methods to analyze differences in song characteristics among juncos from the three regions: (1) Kruskal-Wallis one-way analysis of variance with post-hoc comparisons based on pairwise Mann-Whitney U-tests and the studentized range (Sokal and Rohlf 1995), and (2) linear discriminant function analysis (DFA) to classify individuals to regions based on song features. The latter analysis may be biased towards correctly assigning groups, and we used a jackknifed classification matrix as a more conservative grouping method. All analyses were conducted in Program R (R Development Core Team 2009). Significance thresholds were adjusted to 0.0038 following a Bonferroni correction for multiple comparisons. Results are presented as means ± SE unless labeled otherwise.

RESULTS

Eleven of the 13 features of Yellow-eyed Junco song differed among the three regions (all, \( \chi^2 \geq 11.15, P \leq 0.0037; \) Table 1). The only features that did not differ among regions were the number...
### Table 1. Song features (means ± SE) of Yellow-eyed Juncos from Baja California Sur, Mexico, Arizona, USA, and Oaxaca, Mexico.

<table>
<thead>
<tr>
<th>Song feature</th>
<th>Baja</th>
<th>Arizona</th>
<th>Oaxaca</th>
<th>$\chi^2$ *</th>
<th>$p$ *</th>
<th>Post-hoc *</th>
</tr>
</thead>
<tbody>
<tr>
<td>Song length (sec)</td>
<td>1.78±0.06</td>
<td>1.52±0.05</td>
<td>1.37±0.11</td>
<td>11.29</td>
<td>&lt;0.004</td>
<td></td>
</tr>
<tr>
<td>Syllables per song</td>
<td>11.52±1.02</td>
<td>10.24±0.83</td>
<td>8.18±0.98</td>
<td>17.37</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Number of unique syllables</td>
<td>13.06±0.68</td>
<td>12.26±0.23</td>
<td>7.37±0.60</td>
<td>33.47</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Repeats per syllable</td>
<td>1.22±0.04</td>
<td>3.31±0.20</td>
<td>2.44±0.27</td>
<td>34.73</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Number of trills</td>
<td>1.73±0.25</td>
<td>2.01±0.12</td>
<td>2.00±0.41</td>
<td>2.69</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td>Number of syllables per trill</td>
<td>2.47±0.25</td>
<td>4.45±0.33</td>
<td>3.71±0.61</td>
<td>17.55</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Number of unique notes per trill</td>
<td>1.47±0.22</td>
<td>2.96±0.22</td>
<td>3.30±0.60</td>
<td>22.85</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Number of phrases</td>
<td>2.00±0.13</td>
<td>0.32±0.08</td>
<td>0.50±0.19</td>
<td>34.03</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Number of notes per phrase</td>
<td>12.26±1.37</td>
<td>5.34±0.57</td>
<td>6.95±4.29</td>
<td>12.11</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Peak frequency (Hz)</td>
<td>5,290.46±154.28</td>
<td>4,631.59±99.34</td>
<td>4,384.19±283.61</td>
<td>14.75</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Lowest frequency (Hz)</td>
<td>2,218.49±59.13</td>
<td>2,183.77±63.47</td>
<td>2,126.26±86.06</td>
<td>1.09</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>Highest frequency (Hz)</td>
<td>7,959.87±161.34</td>
<td>7,063.27±173.82</td>
<td>7,749.82±377.44</td>
<td>12.40</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Song bandwidth (Hz)</td>
<td>5,741.38±194.69</td>
<td>4,879.50±184.70</td>
<td>5,623.56±408.50</td>
<td>11.15</td>
<td>&lt;0.004</td>
<td></td>
</tr>
</tbody>
</table>

* $\chi^2$ values for Kruskal-Wallis tests comparing variation in song features among the three regions. Sample sizes for all features except number of notes per phrase were: Arizona, $n = 36$; Baja California, $n = 12$; Oaxaca, $n = 8$. Sample sizes for number of notes per phrase were: Arizona, $n = 13$; Baja California, $n = 16$; Oaxaca, $n = 4$.

1. Significance at $\alpha = 0.05$ when Bonferroni corrected was adjusted to $P \leq 0.0038$.
2. Pairwise post-hoc comparisons are denoted as B-A for Baja vs. Arizona, B-O for Baja vs. Oaxaca, and A-O for Arizona vs. Oaxaca.
of trills per song and the lowest frequency. Four features differed between Oaxaca and Arizona songs (all, \( P < 0.001 \)); Baja California songs were different from those in Arizona for 11 features (all, \( P < 0.001 \)) and were different from Oaxaca songs for six features (all, \( P < 0.001 \); Table 1, Fig. 3). Values for the number of unique syllables and the number of repeated syllables of the Baja California population did not overlap with values from the two mainland populations. Baja California songs had more unique and total syllables per song, and included more phrases than songs from the other two regions. Songs from Baja California had fewer repeats per syllable than those from Arizona or Oaxaca, which coincides with fewer trills and fewer repeated syllables per trill than songs from the two other regions. Baja California songs also were longer and had lower peak and highest frequencies and a narrower bandwidth than Arizona songs. Spectral features of Baja California and Oaxaca songs differed only in terms of peak frequency, while songs from Oaxaca were higher pitched in terms of highest frequency and had a broader bandwidth than those from Arizona.

Discriminant function analysis was based on all song features except number of notes per phrase because many songs from Oaxaca and Arizona lacked phrases. The analysis correctly assigned 87% of the songs to the correct region; 100% were correctly assigned to the Baja California region, 90% were correctly assigned to the Arizona region, and 50% were correctly assigned to the Oaxaca region. Three songs from Arizona were misclassified as from Oaxaca and four Oaxaca songs were misclassified as from Arizona. No Arizona or Oaxaca songs were misclassified as Baja California songs. The Baja California songs were easily distinguishable from Arizona and Oaxaca songs based on the first discriminant axis (97.5% of variance), but Arizona and Oaxaca songs were not easily identifiable based on this axis, nor on the second discriminant axis (2.5% of variance; Fig. 4). Variables with strong loadings on the first axis were song length (1.23) and number of phrases (1.48); those with strong loadings on the second axis were number of trills (1.09) and song length (−2.03; values of all other loadings are in Table 2).

**DISCUSSION**

We found strong systematic differences between songs of *J. p. bairdi* and those of two
FIG. 4. DFA results of song variation of Yellow-eyed Juncos from Arizona, USA (A), Baja California Sur, Mexico (B), and Oaxaca, Mexico (O). Song features included as variables in the DFA included all features (Table 1) except number of notes per phrase. Discriminant score I explains 97.5% of the variance in the data and discriminant score II explains 2.5%. Baja California songs are easily distinguishable based on discriminant score I. Arizona and Oaxaca songs are not easily distinguishable from each other by either score.

mainland Yellow-eyed Junco subspecies (J. p. palliatus and J. p. phaeonotus). The number of unique syllables per song and the number of repeated syllables are diagnostic because there is no overlap in these features between J. p. bairdi and mainland subspecies. In contrast, there were fewer differences between songs of the two mainland subspecies and they were not easily distinguishable from one another through discriminant function analysis.

Vocal features, like other phenotypic traits, are expected to diverge among species and subspecies over time for a variety of reasons (Irwin 2000). One potential explanation for the difference in song is that signal features have diverged in response to unique habitat features (acoustic adaptation hypothesis; e.g., Morton 1975, Boncoraglio and Saino 2007). However, because both mainland and peninsular populations inhabit structurally similar pine-oak forests and arid woodlands (Sullivan 1999), it is unlikely that habitat features would differ sufficiently to account for significant differences in song features.

A more probable explanation for the distinctly different J. p. bairdi song may be that sexual selection pressures have differed for J. p. bairdi relative to mainland populations (e.g., Irwin et al. 2001). It is not clear whether the difference in song would constitute a behavioral barrier to gene flow upon secondary contact among these currently allopatric populations. Song can be used in combination with other tools to identify taxonomic boundaries (Irwin et al. 2001, Päckert et al. 2004, Toews and Irwin 2008), and our results provide initial support for re-evaluating the taxonomic status of J. p. bairdi. However, several key pieces of information are still needed to clarify taxonomic limits. A phylogenetic analysis of the genus Junco by Milá et al. (2007) concluded the genus represents a case of extremely rapid diversification following a postglacial range expansion. Unfortunately, individuals from Baja California Sur (J. p. bairdi) were not included in their analysis, and knowledge of this population’s phylogenetic relationship with the rest of the genus is lacking.

The largest differences in song were between J. p. bairdi and the two mainland subspecies, but our results also show some variation within the songs of mainland Yellow-eyed Juncos. Oaxaca birds sing slightly shorter songs with fewer repeated syllables and shorter trills (fewer syllables per trill) than birds from Arizona. Overall, there appears to be a gradual trend towards increased song complexity (e.g., an increased number of unique syllables and a decrease in the number of repeated syllables) with decreasing latitude among populations included in this study and throughout the ranges of all Junco taxa in western North America (NDP, pers. obs.). Most taxa currently included in the Dark-eyed Junco (J. hyemalis) complex sing simple songs consisting...
of a single trill (a single syllable rapidly repeated), while songs of the "Red-backed" form in northern Arizona (J. p. alticola) frequently consist of two or three trills, or a trill with one or two buzzy notes (Thatcher 1968. Sibley 2000. Christian Nunes recordings, and are apparently intermediate in complexity between the songs of other Dark-eyed Juncos and those of J. p. palliatus. Yellow-eyed Juncos in southeastern Arizona. This trend of increasing complexity may continue south at least to Oaxaca. It is presently unknown whether songs of the Yellow-eyed Junco subspecies south of the Isthmus of Tehuantepec (J. p. fulvescens and J. p. alticola) differ from those of a single trill (a single syllable rapidly repeated), and are apparently intermediate in complexity between the songs of other Dark-eyed Juncos and those of J. p. palliatus. Yellow-eyed Juncos in southeastern Arizona. This trend of increasing complexity may continue south at least to Oaxaca. It is presently unknown whether songs of the Yellow-eyed Junco subspecies south of the Isthmus of Tehuantepec (J. p. fulvescens and J. p. alticola) differ from those north of the Isthmus, and we do not know of any recordings of these taxa. Howell and Webb (1995: 731) describe the song of J. p. alticola, which resides south of the isthmus, as "a varied series of bright chips, usually the last note rising... much like pheaeonotus." Additional recordings from the two southernmost subspecies are needed to understand vocal variation among juncos.

It is clear the song of J. p. bairdi is distinct from that of other Yellow-eyed Junco subspecies, but whether this difference is indicative of an important reproductive barrier is unknown. Still needed are field and molecular studies. Playback experiments are necessary to ascertain whether and how individuals of J. p. bairdi respond to songs from other regions and vice versa. Molecular analyses comparing mitochondrial and nuclear DNA of J. p. bairdi with those groups included in Milá et al. (2007) may provide insight on whether gene flow exists between Baja California juncos and populations on the mainland and, if it does not, how long the population has been genetically isolated and how it is related to the rest of the clade. Promotion to species status may be warranted if field and molecular studies confirm that J. p. bairdi is behaviorally and genetically distinct from mainland juncos.

ACKNOWLEDGMENTS

We thank Carol Beardmore. David Knepper, Richard Erickson, Gary Num, Eduardo Palacios, Victor Anguiano, Western Field Ornithologists, and the Sonoran Joint Venture for organizing and assisting with the expedition to the Sierra La Laguna. We thank the Cornell Laboratory of Ornithology, Borer Laboratory of Bioacoustics. Xeno-Canto, Tom Webber of the Florida Museum of Natural History, S. N. G. Howell, Christian Nunes, Andrew Spencer, and Richard Webber for help in obtaining additional recordings for analysis. We also thank Alexander Cruz and Sarah Wagner for helpful comments on an early version of this manuscript. CDF thanks the National Evolutionary Synthesis Center (NESSCent) for support (NSF EF-0905690) during the final preparation of this manuscript.

LITERATURE CITED


ABSTRACT.—We used Global Positioning System (GPS) satellite transmitters to estimate the breeding home ranges of Turkey Vultures (Cathartes aura) in Saskatchewan, Canada from 2005 to 2009. Breeding ranges calculated using 95% Minimum Convex Polygons (MCP) ranged from 47 to 953 km² and averaged (± SD) 371 ± 340 km². Fixed-kernel home ranges (95%) ranged from 49 to 1,992 km² and averaged 648 ± 731 km². These ranges include both the smallest and largest summer ranges reported for the species. Spatial variation in range size may have been due to differences in availability of food and the quality of the home ranges involved, amplified by the species’ extremely low-cost soaring flight. Adults used all-night perches in varying locations up to 38 km from their nest house while traveling substantial distances to available carcasses to obtain food for their young. Identifying home range sizes for Turkey Vultures is a first step toward understanding how the species is increasing and expanding its distribution in Saskatchewan and elsewhere in Canada.

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Both Old and New World vultures are obligate scavenging birds (Rea 1983, Kirk and Mossman 1998). The scavenging niche has ecological requirements that differ from those of more predatory raptors (Wilbur and Jackson 1983, Mundy et al. 1992). Feeding on carcasses, which can be highly ephemeral and unpredictable (Kelly et al. 2007), often requires breeding vultures to range widely in search of food for their developing young (e.g., Kirk and Mossman 1998). Turkey Vultures (Cathartes aura) exhibit considerable variation in size of home ranges, both within and among geographic areas. Home ranges of non-breeding vultures captured at communal roosts varied from 128 to 1,227 km² in southeastern Minnesota (Tenney 1986), 91 to 482 km² in South Carolina (DeVault et al. 2004), 149 km² in Ohio to 627 km² in Indiana (Arrington 2003), and 149 to 371 km² at Gettysburg in southern Pennsylvania and northern Maryland (Coleman and Fraser 1989).

Turkey Vultures breed from Canada to southern South America, adapt well to grasslands, deserts, deciduous and mixed-deciduous forests, and open and forested tropical lowlands; they are the most widely distributed scavenging bird in the world (Wilbur 1983, Ferguson-Lees and Christie 2001). Individuals can be found year-round in the southern United States, but more northerly breeders migrate from breeding areas to overwinter in the southern United States, Central America, and northern South America (Chapman 1933, Stewart 1977, Kirk and Mossman 1998, Mandel et al. 2011). The most northern breeding populations are in western Canada, including central Saskatchewan. This recent expansion of vulture distribution coincided with an increase in use of long-abandoned farm buildings as nesting sites (Houston et al. 2007).

We have few data on the breeding ecology of Turkey Vultures, apart from locations and characteristics of nest sites, near the northern limits of their range. In particular, we know little concerning size of their breeding home ranges. Our objectives were to: (1) document the size of breeding home ranges of Turkey Vultures in central Saskatchewan, and (2) test the hypothesis that size of home ranges near the periphery of their range would be larger than farther south. Macro-ecological theory suggests that, unless there are abrupt changes in habitat types at the limits of a species’ range, individuals should be more concentrated at the center of the range than near its boundaries (Brown 1984, 1995), possibly because of higher competition for food (Gross and Price 2000). Thus we initially predicted larger home range sizes for Turkey Vultures than previously reported.
METHODS

Study Area.—We tracked vultures at four sites in central Saskatchewan, Canada: two in the Aspen Parkland ecoregion (i.e., a transition zone between southern dry grasslands and northern boreal forest) and two in the Southern Boreal Forest ecoregion (below and above 52.5° N latitude). Most Aspen Parkland is now cultivated; however, native grasslands and woodlands, respectively, are dominated by fescue grassland (Festuca spp.), and quaking aspen (Populus tremuloides) and balsam poplar (P. balsamifera). The Southern Boreal Forest ecoregion is the most diverse biotic region in Saskatchewan (Smith 1996. Thorpe 1999) with an overstory of mixed deciduous (aspen and balsam poplar) and coniferous trees (white spruce [Picea glauca], black spruce [P. mariana], and jack pine [Pinus banksiana]).

Nest Location and Radio Transmitters.—We used radio and newspaper publicity to contact farmers who believed that Turkey Vultures nested on their property. This was critical as many of the farm buildings occupied by nesting vultures were “hidden” by aspen and caragana (Caragana spp.) trees growing in the long-deserted farmsteads.

We captured six adult vultures at their nests and equipped each with an alpha-numeric patagial tag on the left wing and a back-pack style (Steenhof et al. 2007), solar-powered Global Positioning System (GPS) satellite transmitter. We attached four units (#’s 57952, 57953, 65544, and 65545 [Microwave Telemetry, Columbia, MD, USA]), which provided locations almost every hour, to one of the breeding adults at each nest in 2005 and 2007. Two units (#’s 85753 and 85754 [North Star Science and Technology, King George, VA, USA]), providing locations every 3 hrs, were attached to a pair of adults at a single nest in 2009. All six transmitters had an accuracy of ± 10–15 m. Transmitters for four adult vultures recorded the daily maximum elevation above ground and the time when this occurred. We used DNA from feathers to identify individuals as male or female (Health Gene Laboratories, Toronto, ON, Canada) for a pair of adults captured at the same nest site (male # 85753 and female # 85754).

Breeding Home Ranges.—The 2005 and 2007 migration paths to Venezuela and back appear in Mandel et al. (2011). We used locations after birds returned to Saskatchewan (Fig. 1) during weeks when adults were incubating eggs or feeding young (Jun–Aug) to calculate home range size. We used 95% Minimum Convex Polygon (MCP; White and Garrott 1990) and 95% fixed-kernel (Worton 1989, 1995) methods, using the Home Range Estimator (HRE) program of Rogers and Carr (1998) available for ArcView 3.2 (ESRI 2005). The 95% kernel contour is believed to most accurately reflect home range size because it minimizes biases caused by inclusion of outlying locations in the range estimate (Kernohan et al. 2001, Hasselblad and Bechard 2007). GPS telemetry data generated large data sets, including multiple locations (up to 24) on single days. We re-sampled all data sets to 120 randomly chosen points to reduce autocorrelation for computing fixed-kernel home ranges, which are utilization distributions of use sensitive to temporal autocorrelation (Schoener 1981; Swihart and Slade 1985a, b; Ackerman et al. 1990). We computed the smoothing parameter (h) of fixed-kernel ranges as the optimum value with reference to a known standard distribution (i.e., Silverman 1986; Worton 1989, 1995). This was the square root of the mean variance in x and y coordinates divided by the sixth root of the number of points following a standard bivariate normal probability density function (Rogers and Carr 1998). We used this method because, after 1 week of brooding, each adult vulture typically visited the nest site once daily, and h-ref is expected to be effective if the underlying use distribution is unimodal (Worton 1995; Rogers and Carr 1998). Statistical analyses were performed in R Version 2.10.0 (R Foundation for Statistical Computing 2009). Data presented are means ± SD.

RESULTS

We obtained an average of 988 ± 392 satellite-tracking locations per bird per year (Table 1). Home range size estimated using the 95% MCP method ranged from 47 to 953 km², averaging 371 ± 340 km² (Table 1). Fixed-kernel home ranges (95%) ranged from 49 to 1,992 km² and averaged 648 ± 731 km² (Table 1). Fixed-kernel ranges calculated from 120 randomly selected points to minimize temporal autocorrelation in each telemetry location did not differ from fixed-kernel home ranges calculated using all points available for a bird (paired two-sample t-test, t = -1.32, P = 0.23). Mean home-range size calculated using the 95% MCP and 95% fixed-kernel methods also did not differ (paired two-sample t-test, t = -0.28,
TABLE 1. Annual breeding home range size of six Turkey Vultures in central Saskatchewan, Canada. 2005-2009. Estimates of 95% fixed-kernel home ranges were based on a random subsample of 120 locations (all birds). ID = patagial tag and transmitter number.

<table>
<thead>
<tr>
<th>Vulture ID (Year)</th>
<th>Dates</th>
<th>M/F</th>
<th>n</th>
<th>95% MCP (km²)</th>
<th>95% Fixed kernel (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>H2 57952 (2005)</td>
<td>19 Jun-13 Aug</td>
<td>Unk</td>
<td>945</td>
<td>953</td>
<td>1,992</td>
</tr>
<tr>
<td>T2 65545 (2007)</td>
<td>17 Jun-19 Aug</td>
<td>F</td>
<td>1,320</td>
<td>416</td>
<td>567</td>
</tr>
<tr>
<td>T3 85753 (2009)</td>
<td>22 May-28 Aug</td>
<td>M</td>
<td>331</td>
<td>47</td>
<td>49</td>
</tr>
<tr>
<td>T4 85754 (2009)</td>
<td>22 May-28 Aug</td>
<td>F</td>
<td>774</td>
<td>47</td>
<td>75</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td></td>
<td></td>
<td>988 ± 392</td>
<td>371 ± 340</td>
<td>648 ± 731</td>
</tr>
</tbody>
</table>

P = 0.98). Home ranges decreased in size from 2005 to 2009 (fixed-kernel home range size vs. year, t = 3.98, P = 0.016, r² = 0.80) (Table 1).

We received good signal reception during early incubation, 23-30 May for the pair of adults captured at the same nest site (male # 85753 and female # 85754), and for the female during brooding, 30 June–4 July (Figs. 2, 3). Transmitter signals were not received from male # 85753 throughout most of June and the entire brooding period in early July. Both adults took turns incubating until the eggs hatched between 25 and 30 June (Fig. 2); brooding then became intensive by the female for about 18 hrs per day including each night through 4 July (Fig. 3). Brooding ceased entirely after 10 July and a daily feeding visit by each adult was so brief that it was rarely recorded near the nest house. All-night perch sites, rarely used more than once, after brooding ceased, were unexpectedly distant for all 6 adults: up to 37.8, 38.8, 17.7, 29.7, 7.5, and 15.9 km from the nest house with young (Table 2). Vultures ascended to 558, 902, 681, and 627 m above the altitude of the nest house when searching for carcasses (Table 3).

DISCUSSION

There was considerable variation in breeding home range size of the Turkey Vultures we tracked; we recorded some of the smallest and largest breeding ranges recorded for the species. What governs home range size can be complex (McLoughlin and Ferguson 2000, Peery 2000); however, a wide-ranging survey of home range size in birds (Rolando 2002) suggests food availability is the primary determinant of avian range size and all other factors are secondary. We suggest heterogeneity in food availability may explain variation in the breeding range size for the vultures we studied. For example, the small breeding range sizes of vultures # 85753 and # 85754, a mated pair tracked in 2009, were in the North Saskatchewan River Valley (Fig. 1), a relatively productive riparian area; these vultures may have had greater access to food than the other four birds in our study. It also is possible that carrion availability changed among years, as we observed larger breeding ranges earlier in the 4-year study than in later years. Large home range sizes are made possible, in part, by the species' extremely low-cost soaring flight (cf. Mandel et

TABLE 2. Night perches of six Turkey Vultures occupying home ranges in central Saskatchewan, Canada, 2005–2009. Distances (km) are from the known nest house to all-night perch sites.

<table>
<thead>
<tr>
<th>Patagial tag</th>
<th>HO</th>
<th>H2</th>
<th>H8</th>
<th>T2 female</th>
<th>T3 male</th>
<th>T4 female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transmitter #</td>
<td>57953</td>
<td>57952</td>
<td>65544</td>
<td>65545</td>
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<td>85754</td>
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HOURS OF HIGHEST FLIGHT (CST):

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<td>145</td>
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</table>

Mean time (CST) of highest flight (hrs) | 1324 | 1429 | 1343 | 1411 |

al. 2008, 2011), which significantly reduces the cost of searching large areas for carrion.

We found published records of only three vultures for which breeding home ranges were calculated. The two vultures tracked during the breeding season near Gettysburg had 95% MCP home ranges with a mean of either 69.4 km² (Coleman and Fraser 1989) or 126.0 km² (Coleman 1985). Arrington (2003) captured one adult female vulture on her nest at the Pigeon River Wildlife Area, northeastern Indiana; it had a 100% MCP of 557 km² and a 90% kernel of 9.9 km² based on 342 satellite transmitter readings. Our mean 95% MCP of 371 km² was similar. The size of our Saskatchewan home breeding ranges was uniquely limited to locations of known breeding vultures from incubation through fledging of young. Comparisons with other studies of the home-range size of non-breeding Turkey Vultures (e.g., Tenney 1986, and those studied by Coleman and Fraser 1989 and DeVault et al. 2004) are less appropriate.

Tracking both members of a pair of Turkey Vultures (male # 85753 and female # 85754) during incubation and brooding provided new information. Both had relatively small and virtually identical home ranges. Each would incubate for either one or two consecutive nights when regular signals were received from both during 23-30 May (Fig. 2). However, brooding was exclusively by the female at night during 30 June-4 July, but with 6 hrs respite in mid-day (Fig. 3); signals were not received from the male during this time. Brooding by the female ceased after 27 hrs of continuous brooding on a notably cool and rainy day, 10 July (data from Environment Canada, http://climate.weatheroffice.gc.ca).

Identifying size of home ranges for Turkey Vultures near their northern range limits increases our understanding of how the species is adapting to recently occupied areas in Saskatchewan and elsewhere in Canada. We believe the recent human depopulation of rural areas, together with abandonment of farm buildings, has had a crucial role in increasing numbers of successfully nesting Turkey Vultures. Vulture nests were rarely discovered prior to the 1980s, and were restricted to difficult-to-find caves in badlands in extreme southern Saskatchewan and along major river valleys through southern and central Saskatchewan with occasional single-year use of cavities within large brush-piles. Northward range extension is not involved, but in 1982-1984, the first four vulture pairs were found in deserted buildings in central Saskatchewan and vultures were no longer relying on natural caves for nesting.
FIG. 1. Telemetry locations and annual breeding home ranges (95% fixed-kernel) of six Turkey Vultures (satellite identification number indicated) in central Saskatchewan, Canada, 2005-2009. Nest sites (abandoned buildings) are indicated as dotted squares. Vultures # 57953 and # 65544 shared the same site in different years; vultures # 85753 and # 85754 were a mated pair.

(Houston et al. 2007). Vultures were soon breeding widely in deserted buildings on farms throughout the Aspen Parkland and southern Boreal Forest ecoregions (Houston and Terry 2003). For example, vultures first nested in the 11,012 km$^2$ Saskatoon Bird Area in 2002 (Houston et al. 2002) and most farmers in Saskatchewan have reported vultures only during the past decade.

These increases in vulture nesting activity may also be in response to gradual increases in availability of ungulate carrion, related to documented province- and Canada-wide increases in wildlife-vehicle collisions (especially with deer) on highways (Tardif and Associates 2003). The number of reported collisions with wildlife in Saskatchewan from 1988 to 2009 increased from 3,695 to 13,052 with a particularly marked rise in the past decade (Traffic Information System, Saskatchewan Government Insurance, Regina, Canada). Short-term increases in carrion supply are also coincident with management actions, enacted in 2002, to control Bovine Spongiform Encephalopathy (BSE); these actions closed

The lack of a substantial increase in the breeding home range size of Turkey Vultures near the northern limits of its range suggests food resources there are not appreciably different from those farther south. It is also possible these limits are set by distances the birds travel twice annually to and from southern wintering areas (cf. Mandel et al. 2008, 2011). “Western North America populations of Turkey Vultures forego feeding en route, at least for most of their journey” (Bildstein 2006:191) and “the condition of adult migrants [in Venezuela] was below average in October and November following migration from the breeding grounds” (Kirk and Gosler 1994:933). Physiological and aerodynamic constraints on fat loading prior to migration may preclude longer seasonal movements. Studies of the size of breeding home ranges of Turkey Vultures, especially in the Neotropics of Central America, northern South America, and the temperate zone of southern South America, are warranted.

ACKNOWLEDGMENTS

We thank M. J. Mossman and an anonymous reviewer for helpful comments. Special appreciation is extended to Don Forbes and over a hundred Saskatchewan farmers for their co-operation and interest, and to Brent Terry and Michael Blom for the many days and miles involved in field work. PDM was supported by a grant from the Natural Sciences and Engineering Research Council (Canada). This manuscript is Hawk Mountain Contribution to Conservation Science, Number 198.

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FIG. 3. Attentiveness of female # 85254 while brooding downy young, 30 June-4 July 2009. Black = present at nest site.
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CONSPECIFIC BROOD PARASITISM AND NESTING BIOLOGY OF MANDARIN DUCKS (AIX GALERICULATA) IN NORTHEASTERN CHINA

QIU-XIANG DENG,¹² HAI-TAO WANG,¹³ DI YAO,¹ XING-YANG WANG,¹ MING-JU E,¹ TUO WANG,¹ AND WEI GAO¹³

ABSTRACT.—Conspecific brood parasitism (CBP) is a widespread alternative female reproductive tactic in birds. We monitored CBP and nesting biology of Mandarin Ducks (Aix galericulata) using nest boxes for six breeding seasons in Zuojia, northeast China. CBP occurred commonly (46.2% of completed clutches) during the study and frequency was positively associated with nest densities. The frequency of CBP declined as the nesting season progressed. On average, 2.5 females laid eggs in each parasitized nest. There were significant differences in clutch initiation dates and mean laying period between parasitized and un-parasitized nests; no difference was detected for the mean incubation period. Clutch size for un-parasitized nests decreased with advancing incubation period, but not for parasitized nests. The hatching rate for eggs in successful nests was 87.1%, and no significant difference was detected between parasitized and un-parasitized nests. The average number of ducklings that hatched from successful un-parasitized and parasitized nests was 8.4 and 15.4, respectively. Nest desertion was the main cause for nest failure and sibling trampling was the only cause of duckling loss before departure from nests. Received 9 September 2010. Accepted 26 February 2011.

Conspecific brood parasitism (CBP), a widespread alternative female reproductive strategy, has been documented for 236 avian species (Yom-Tov 2001); several potential benefits may enhance its occurrence. Females that lay eggs in nests of others could avoid the physiological costs and dangers associated with incubation and parental care (Andersson 1984). Nest parasitism may be associated with an increase in total fecundity (McRae 1998, Ahlund and Andersson 2001). Parasitism could benefit females that cannot find a suitable nest site or have lost a nest due to destruction (Semel et al. 1988, Lank et al. 1989). Dispersing eggs into several nests may also eliminate the risk of a failed clutch jeopardizing their entire reproductive effort (Payne 1977, Brown and Brown 1988). CBP is disproportionately common among waterfowl relative to other taxa (Eadie et al. 1998). Waterfowl have precocial young that require less post-hatch parental care than altricial young, which may minimize costs to hosts, and possibly explain the prevalence of this behavior (Roy Nielsen et al. 2006a).

CBP behavior of Wood Ducks (Aix sponsa) has received substantial attention (Heusmann et al. 1980, Semel and Sherman 1986). The costs and benefits to parasitic females and their hosts, and the ecological factors influencing the frequency of CBP within and among Wood Duck populations are well documented (Semel and Sherman 2001, Roy Nielsen et al. 2006b). High levels of CBP may lead to increased levels of nest desertion (Jones and Leopold 1967, Semel and Sherman 1986), reduced hatching success of eggs or fledging success of young (Semel et al. 1988, Semel and Sherman 2001), and higher predation risk and energetic costs due to longer incubation periods (Hepp et al. 1990, Roy Nielsen et al. 2006a). Frequency of CBP has been associated with nest densities (Clawson et al. 1979, Haramis and Thompson 1985). A possible benefit of CBP to hosts is higher inclusive fitness, if parasites are relatives (Roy Nielsen et al. 2006b).

The Mandarin Duck (Aix galericulata) is the most widely introduced waterbird within the African-Eurasian Migratory Waterbird Agreement area and perhaps in the world due to their attractive appearance (Rehfisch et al. 2006). An introduced population has been breeding in Britain since the 1930s (Savage 1952). Native Mandarin Ducks breed in Russian Ussuriland in Amur, Khabarovsk, and Primorye regions as far west as Zeya Estuary, northern China, Sakhalin Island, Kunashir in Kuril Islands, and in Hokkaido, the most northerly of Japan’s main islands (Kear 2005).

The Mandarin Duck incubates clutches that vary greatly in size. Davies and Baggott (1989a,
b) reported the variable clutch size of Mandarin Duck was a function of CBP, and provided information about egg-laying, clutch size, and incubation for the introduced population in Britain. The literature on Mandarin Ducks provides information on breeding dates, descriptions of eggs, clutch size, nest-site, and parental care (Clawson et al. 1979, Shurtleff and Savage 1996, Li et al. 2009, Jin et al. 2010). However, no studies of CBP and updated nesting biology of the Mandarin Duck are available for native populations.

The objectives of our study were to: (1) provide information on aspects of CBP and nesting biology of the Mandarin Duck, (2) identify conditions which facilitate occurrence of CBP, and (3) provide a better understanding of the behavioral traits and their effects on productivity of the species.

**METHODS**

**Study Area.**—We studied Mandarin Ducks for six breeding seasons (2004–2009) at Zuojia Nature Reserve in northeast China. The Zuojia Nature Reserve ranges from the eastern Chang Bai Mountains to the western plain (126°1’–127°2’ N, 44°6’–45°5’ E), and ranges from 200 to 530 m asl. The region is subject to an eastern monsoon climate, characterized by hot, dry summers and cold, snowy winters. The forest type within the reserve is secondary growth: trees were ~40 to 50 years of age.

**Field Procedures.**—No nests of Mandarin Ducks were found in Zuojia prior to this study although the species was recorded as a summer visitor. We installed nest boxes in the study area in 2004 and Mandarin Ducks began to use them. Nest boxes were constructed from rough-cut boards and assembled with exterior nails or deck screws. The internal dimensions of all boxes were: 50 cm deep with a 35 × 35-cm² floor and a 12.5- or 15-cm diameter entrance hole near the top. The roof of each nest box was designed to be waterproof and the bottom was designed to permit drainage. The roof and body of each nest box were placed together with hinges, and a hook and ring were used to prevent the roof from being opened unintentionally. A slat of wood was nailed to the back of every nest box to provide a ledge for nest placement. Nest boxes were attached to trees with four spikes and a section of wire. Nest boxes were placed ~8–13 m above ground with 50–150 m between adjacent boxes. We replaced nest boxes when they were destroyed or unusable. Numbers of boxes monitored were 52, 56, 61, 68, 77, and 80 for the years from 2004 to 2009, respectively.

We checked nest boxes at intervals of 5–7 days while attempting to first locate Mandarin Duck eggs in boxes, and then at 1–2 day intervals during the remaining egg-laying period. Eggs were numbered consecutively with indelible marker to monitor egg losses as well as newly deposited eggs. We prolonged the visiting interval to 6–7 days during incubation to avoid female disturbance and, on days of expected hatching, we shortened the visiting interval to 1–2 days. We minimized disturbance caused by researchers and did not capture incubating females to mark them in the study. We designated nests in which two or more eggs were added within a day or clutch size more than 12 eggs (using the published clutch size of the species as criteria) as parasitized (Semel and Sherman 1992, Lyon 2003). Nests with ≤12 eggs were considered non-parasitized. We estimated clutch initiation dates of nests that contained several eggs from the earliest known point in the nesting sequence. We back-dated the nest assuming a laying rate of one egg per day for nests first located with fewer eggs than the days elapsed since the previous nest box check (when the box was still empty). We assumed the nest was parasitized and was initiated on the first day after boxes were last known to be empty for nests first located with more eggs than days elapsed since the previous nest box check.

A nest was classified as successful if nestlings were observed, or egg shell fragments were found in box on day of expected hatching. We classified a nest as abandoned if it contained undamaged eggs and adults were absent for >5 days. We collected unhatched eggs for analysis to ascertain fertilization. We recorded nesting chronology for all active nest boxes and attempted to identify the causes of failed nests using a combination of clues whenever possible.

**Statistical Analysis.**—We defined incomplete clutches as those that did not enter the incubation stage, and a final clutch size could not be ascertained. We defined ‘combined clutch size’ as the number of eggs laid into any single nest box as a completed clutch; ‘clutch size of unparasitized’ implied that all eggs were laid by a single female, and ‘clutch size of parasitized’ implied that eggs in a completed clutch were laid by two or more females. We assumed clutches...
that contained a full lining of down were incubated, and presence of warm eggs and repeated flushing of a bird from the box confirmed this assumption. We removed nests that were deserted during the laying period (incomplete clutches) in calculating clutch size. We converted nest initiation date to Julian day before analysis.

The independent sample t-test was performed to compare clutch initiation dates and nest characteristic variables between un-parasitized and parasitized nests. We used linear regression to examine whether clutch size was related to clutch initiation date. We analyzed the relationship between frequency of CBP and nest densities using Spearman correlation coefficients. SPSS for Windows, Version 14.0 (SPSS Science, Chicago, IL, USA) was used for statistical analyses. Means ± SD are presented.

RESULTS

Conspecific Brood Parasitism.—Forty-two of 410 nest-box years were occupied by Mandarin Ducks with an average of 7.0 ± 5.4 (n = 6 yrs) boxes used per year (range = 1 to 15 nests annually). CBP occurred commonly in Mandarin Ducks. Eighteen of 39 (46.1%) nests with a complete clutch were parasitized. Frequency of CBP by Mandarin Ducks was positively correlated with nest densities (Spearman's correlation: \( r = 0.880, n = 6, P = 0.021 \)). We estimated that 2.5 ± 0.7 (n = 15) females laid in each parasitized nest as indicated by eggs appearing per day.

Nest Chronology.—Clutch initiation dates ranged from 22 April to 11 June (n = 41) with two laying peaks (Fig. 1). Clutch initiation dates for un-parasitized (n = 21) and parasitized nests (n = 18) differed (t = 2.594, \( P = 0.014 \)). CBP occurred more frequently during the early portion of the breeding season. The median first-egg date for parasitized nests was 5 May (n = 18), and was 17 May for un-parasitized nests (n = 21). Eggs of a clutch in individual nests were laid on consecutive days or at longer intervals from 1 to 6 days. The laying period differed between un-parasitized (n = 21) and parasitized (n = 18) nests (t = -4.126, \( P < 0.001 \)), and was 11.9 ± 2.4 days and 15.3 ± 2.9 days, respectively. The mean incubation period for successful nests was 32.7 ± 1.4 days (n = 23, range = 31–36 days); no significant difference was detected between un-parasitized (n = 16) and parasitized (n = 7) nests (t = 0.031, \( P = 0.98 \)).

Clutch Size.—Three nests were deserted during egg laying and incomplete clutches ranged from one to six eggs. Clutch size of complete un-parasitized (n = 21) and parasitized nests (n = 18) differed (t = -10.787, \( P < 0.001 \)) and was 9.7 ± 1.6 eggs (range = 7–12), and 18.8 ± 3.2 eggs (range = 15–25), respectively (Table 1). The combined clutch size was 14.0 ± 5.1 (n = 39). Clutch size for un-parasitized nests decreased as the nesting season progressed (\( \beta = -0.730, F_{1,20} = 21.625, P < 0.001 \)), but not for parasitized nests (\( \beta = -0.255, F_{1,17} = 1.112, P = 0.307 \)).

Nesting Success.—Thirty-nine of 42 nest attempts reached a complete clutch size during the breeding seasons of 2004–2009 (Table 1), and 23 nests successfully produced young that left the nest box. Failure of 19 unsuccessful nests primarily occurred during incubation (84.2%) following by the egg laying period (15.8%); no
TABLE 1. Reproductive parameters of Mandarin Ducks during the 2004–2009 breeding seasons in Zuojia Natural Reserve, northeastern China.

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<td>42</td>
</tr>
<tr>
<td>Number of nests with full clutch size</td>
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<td>18</td>
<td>39</td>
</tr>
<tr>
<td>Number of nests successful</td>
<td>16</td>
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<td>23</td>
</tr>
<tr>
<td>Number of nests that ducklings left</td>
<td>16</td>
<td>7</td>
<td>23</td>
</tr>
<tr>
<td>Clutch size (mean ± SD)</td>
<td>9.7 ± 1.6</td>
<td>18.8 ± 3.2</td>
<td>14.0 ± 5.1</td>
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<tr>
<td>Range, n</td>
<td>7-12, 21</td>
<td>15-25, 18</td>
<td>7-25, 39</td>
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<tr>
<td>Hatching rate in successful nests (%)</td>
<td>88.7 ± 3.2</td>
<td>83.5 ± 3.9</td>
<td>87.1 ± 12.0</td>
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<td>Ducklings that left boxes (%)</td>
<td>100.0 ± 0.0</td>
<td>96.6 ± 1.7</td>
<td>98.9 ± 2.8</td>
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<tr>
<td>Number of ducklings left per nest</td>
<td>8.4 ± 0.7</td>
<td>15.4 ± 1.3</td>
<td>10.5 ± 4.4</td>
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</tbody>
</table>

* Only nests that ducklings left successfully were included.

Causes for Egg and Duckling Loss.—Nest desertion was the main cause for egg failures, accounting for 72.8%, followed by non-fertilization (11.4%), and human disturbance (11.1%); the remaining egg loss was due to embryo death and unknown reasons (Table 2). Five ducklings from three parasitized nests with large number of ducklings died before leaving the nest; we believe sibling trampling was the only cause of duckling loss before leaving nests.

DISCUSSION

Studies examining population-level frequencies of parasitically-laid eggs have reported brood parasitism increases with increasing nest densities in several species of waterfowl (Clawson et al. 1979, Heusmann et al. 1980, Haramis and Thompson 1985, Eadie et al. 1998, Robertson 1998, Waldeck et al. 2004). CBP occurred commonly among Mandarin Ducks in our study. CBP in this Mandarin Duck breeding population should not be due to a lack of nest resources because ~43.6 ± 7.1% (n = 6) nest boxes were unused annually excluding boxes used by Mandarin Ducks and other birds in the study area. Our results are in agreement with the density hypothesis because frequency of CBP was positively correlated with number of boxes occupied by Mandarin Ducks.

Native Mandarin Ducks in China breed later than the introduced population in Britain. Some introduced Mandarin Ducks have completed clutches in late March. However, native Mandarin Ducks in northeast China begin to lay in late April, which is probably related to latitudinal geographic variation. Grice and Rogers (1965) found CBP by Wood Ducks was more prevalent in early-season nests rather than late-season nests. Davies and Baggott (1989a) reported similar

TABLE 2. Causes of egg loss for nesting Mandarin Ducks during the 2004–2009 breeding seasons in Zuojia Natural Reserve, northeastern China (n = 316 eggs).

<table>
<thead>
<tr>
<th>Causes</th>
<th>Un-parasitized nest* (n = 89)</th>
<th>Parasitized nests (n = 227)</th>
<th>Combined (n = 316)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs unfertilized, %</td>
<td>19.1 (9)*</td>
<td>8.4 (6)*</td>
<td>11.4</td>
</tr>
<tr>
<td>Embryos dead, %</td>
<td>11.2 (3)*</td>
<td>0.4 (1)*</td>
<td>0.9</td>
</tr>
<tr>
<td>Nest desertion, %</td>
<td>53.4 (6)*</td>
<td>79.7 (10)*</td>
<td>72.8</td>
</tr>
<tr>
<td>Nest tree deforested, %</td>
<td>12.4 (1)*</td>
<td>0</td>
<td>7.6</td>
</tr>
<tr>
<td>Female dead, %</td>
<td>3.6 (1)*</td>
<td>0.9 (2)*</td>
<td>1.2</td>
</tr>
<tr>
<td>Unknown reasons, %</td>
<td>2.2 (2)*</td>
<td>2.2 (2)*</td>
<td>2.2</td>
</tr>
</tbody>
</table>

* Three nests with < seven eggs were categorized as un-parasitized.
* Numbers in parentheses are the number of failed nests.
findings for Mandarin Ducks, as clutches in late March and early April exceeded 20 eggs; however, in late May clutches consisted of 10 eggs or less. We found two obvious laying peaks in the Mandarin Duck population studied, and most CBP occurred in nests initiated early in the breeding season (Fig. 1). This supports the hypothesis that females may adopt a mixed reproductive strategy of combining early parasitism with late nesting (Trivers 1972, Lyon and Eadie 2008).

Un-parasitized nests took longer to complete than anticipated with a laying rate of one egg per day, while parasitized nests took a shorter time than expected. We estimated that 2.5 females laid eggs in the same box based on eggs appearing per day, which was similar to the findings of Davies and Baggott (1989a). Mandarin Ducks laid on consecutive days or at longer intervals ranging from 1 to 6 days. Thus, it is possible that a female laying parasitically at one nest site was responsible for the break in laying at another, as has been demonstrated for marked individuals of Wood Ducks (Clawson et al. 1979).

Consistent with reports of others (Campbell and Ferguson-Lees 1972, Cramp 1977, Lever 1977), clutch size for un-parasitized nests of Mandarin Ducks ranged from seven to 12 eggs in our study. The recorded maximum clutch size for the species in a single box was 36 eggs (Davies and Baggott 1989a), while the maximum clutch size was 25 eggs in our study. This variability may be associated with the number of females that laid eggs in the same box.

The hatching rate for eggs in all successful nests of Mandarin Ducks was 87.1% in our study, which was higher than the 70% reported for the species by Davies and Baggott (1989b), and also higher than ~60% for Wood Ducks (Davis 1978, Zipko 1979, Moore 1981, Haramis and Thompson 1985, Semel et al. 1988). Lower hatching success of Wood Ducks was frequently associated with factors caused by CBP including nest desertion and inefficient incubation, which may ultimately influence the reproductive success at the population level (Semel et al. 1988). Our results indicate the parasitic behavior in the Mandarin Duck breeding population studied has not reached the problematic levels reported for Wood Duck populations.

Ten parasitized and six un-parasitized nests received no subsequent incubation due to nest desertion in our study, which has also been reported for nest parasitism of Wood Duck nests (Jones and Leopold 1967, Haramis and Thompson 1985, Semel et al. 1988, Roy et al. 2009). Several other factors may also affect desertion frequency of parasitized nests, including disturbance of laying or incubating females by parasitic females (Davis 1978, Semel and Sherman 1986) and the large number of eggs laid (Moore 1981, Semel and Sherman 1986). Nest desertion can also occur in response to factors unrelated to parasitism, including nest predation (Hill and Sealy 1994, Hosoi and Rothstein 2000), human disturbance (Rothstein 1975), broken or leaking eggs (Scott and Lemon 1996), and nest-site competition (Semel and Sherman 2001). Nest predation and broken or leaking eggs were not observed in our study, and the high rate of desertion might relate to nest parasitism. However, factors other than parasitism including disturbance from repeated nest inspection by researchers and interspecies competition for nest sites can not be excluded. Further study is required to identify factors responsible for nest desertion in this breeding Mandarin Duck population.

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LITERATURE CITED


Spatial Variation in Clutch Size and Egg Size within a Colony of Whiskered Terns (Chlidonias hybrida)

PIOTR MINIAS,1,2 KRZYSZTOF KACZMAREK,2 TOMASZ JANISZEWSKI,1 AND ZBIGNIEW WOJCIECHOWSKI1

ABSTRACT.—Egg and clutch size of Whiskered Terns (Chlidonias hybrida) in relation to their location within the colony were investigated at Jeziorsko Reservoir, central Poland. All nests (n = 125) in the colony were individually marked and mapped using a Global Positioning System. Four nest clusters were distinguished within the colony based on the patchy distribution of floating vegetation which delineated potential nesting areas. Early breeding Whiskered Terns nested in more central and denser parts of nest clusters and late breeders nested in more peripheral zones of the clusters (trend analysis: $F = 20.47$, df = 1, $P < 0.001$). Pairs which nested closer to the centers of clusters had larger clutch sizes (trend analysis: $F = 5.70$, df = 1, $P = 0.019$), but there was no relationship between clutch size and distance to the colony center ($F = 0.38$, df = 2, $P = 0.69$). Edge clutches had higher coefficient of variation in egg volume in comparison to more central clutches (trend analysis: $F = 5.07$, df = 1, $P = 0.028$). Terns nesting in intermediate densities laid eggs of the highest length and volume (trend analysis: $F = 7.17$, df = 1, $P = 0.009$; $F = 6.35$, df = 1, $P = 0.014$, respectively). We suggest that establishment of particular nest clusters in the Whiskered Terns colony at Jeziorsko Reservoir followed a central-periphery model.

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Breeding individuals of different quality expressed by age, experience or physical condition may not be evenly distributed across colonies of waterbirds (Coulson 1968a). Nesting sites within a colony usually differ in attractiveness and intense competition may occur between pairs for favored sites (Birkhead and Furness 1985). Distribution of breeding pairs within the colony and nesting in higher densities should provide more efficient protection against predators and promote higher breeding success (Velando and Freire 2001). Several studies have demonstrated reduced egg/chick losses in the center of waterbird colonies (Gotmark and Andersson 1984, Oro 1996, Yorio and Quintana 1997). Individuals of higher quality should dominate weaker conspecifics and relegate them to peripheral zones; thus, they are expected to occupy the most favorable sites in colonies (Porter 1990). However, not all species of waterbirds follow the central-periphery model of nest distribution. A central-satellite model was developed to explain spatial patterns characteristic for colonial waterbirds breeding in heterogeneous habitats (Velando and Freire 2001). This model assumes low-quality pairs nest around the most favorable sites occupied by high-quality pairs to achieve extra-pair copulations or acquire a better site or mate in succeeding years. The central-satellite model of nest distribution has been reported for European Shag (Phalacrocorax aristotelis) (Velando and Freire 2001), Pelagic Cormorant (P. pelagicus) (Siegel-Causey and Hunt 1986), and Blue-footed Booby (Sula nebouxii) (Nelson 1978).

Spatial variation in breeding success and chick survival rates has been described for several colonial waterbirds (e.g., Coulson 1968a, Drexhimer and Southern 1974), but studies of egg and clutch size are lacking. High repeatability and heritability of egg size in comparison to other reproductive characteristics such as laying date suggests its considerable adaptive significance (Lessells et al. 1989). Egg size of several larid species exerted a profound impact on offspring performance and survival rates (Davis 1975, Thomas 1983, Bolton 1991). Egg size has also been found to increase with age and breeding experience of females (Nisbet et al. 1984, Syedman and Emslie 1992) and has been correlated with morphological indices of maternal quality, including size or mass (Bolton et al. 1993). Clutch size is also known to be affected by condition of females (Rowe et al. 1994), which has been confirmed in larids (Coulson and Porter 1984). Both clutch size and egg size have been suggested as proxies of parental quality (Amundsen and Stokland 1990, Slagsvold and Lifjeld 1990) and their spatial variation within the colony is assumed to reflect distribution of different-quality breeding pairs.

The Whiskered Tern (Chlidonias hybrida) is a
cosmopolitan species characterized by fluctuating numbers and scattered distribution (Cramp and Simmons 1997). It is classified as a species of unfavorable Pan-European conservation status and as a conservation priority by the European Union Wild Birds Directive (BirdLife International 2004). There are few reliable data on the breeding ecology of Whiskered Terns, which precludes application of appropriate conservation measures (Bakaria et al. 2002, Paillisson et al. 2006). The goal of our paper is to investigate spatial variation in clutch and egg size within a colony of Whiskered Terns in central Poland. Whiskered Terns nest on beds of floating vegetation (Paillisson et al. 2006), which is a highly homogenous habitat and its quality is expected to have a negligible role in choice of nest sites within the colony. Therefore, we expected central-periphery distribution of nesting pairs resulting in earlier breeding and higher clutch/egg size in central parts of the colony or particular nest clusters.

METHODS

Study Area.—The research was conducted at Jeziorisko Reservoir in central Poland (51° 40' N, 18° 40' E). Jeziorisko is one of the largest reservoirs in Poland with respect to water surface, which oscillates between 17.6 km$^2$ in autumn to 42.3 km$^2$ during highest water level in spring. Suitable habitats for Whiskered Terns do not appear at the reservoir before the second half of June, due to water management policies resulting in high water levels earlier in the season. The colony of Whiskered Terns studied was at the western shore of the reservoir, in the proximity of the village Tomislawice. Nests were on floating vegetation dominated by amphibious bistort (Polygonum amphibium). The distribution of vegetation within the colony was patchy and four separate beds of floating vegetation were distinguished (Fig. 1). Beds of floating vegetation were separated by much deeper open-water channels and we distinguished four separate nest clusters (A–D, Fig. 1). The mean distance between centers of neighboring nest clusters was 125 m. There were 21 to 44 nests in each cluster.

Field Procedures.—We visited the colony every 10 days from 20 June 2009, when the first nests were initiated, throughout the entire breeding season. The last clutches were initiated between 20 July and 1 August. We assigned initiation of each clutch to particular 10-day periods. We recorded 125 active nests, all of which were individually marked. The length (L) and breadth (B) of all 312 eggs found in the colony were measured with calipers to the nearest 0.1 mm by the same person. Each egg was marked with indelible ink. Egg volume was calculated using the formula: \( V = 4.866 \times 10^{-4} \times L \times B^2 \) (Coulson 1968b). Mean within-clutch values of all egg size characteristics were used in the analyses to avoid pseudo-replication (Barbirua and Zielinski 1990). One clutch with an atypically small egg was excluded from the data set, following suggestions of Zar (1996) on sample homogeneity. The within-clutch variation in length, breadth, and volume of eggs was expressed as the within-clutch coefficients of variation (CV) calculated with the formula: \( CV = SD \times 100/Y \), where SD is the standard deviation and Y is the mean within-clutch value of egg measurements. Calculations of the coefficients of variation are known to be biased for small sample sizes (Sokal and Rohlf 1995) and we applied the correction: \( CV_{\text{adjusted}} = (1+1/4n) \times CV \), where n is clutch size. Location of all nests within the colony (\( n = 125 \)) was mapped using a hand-held Global Positioning System (GPS) unit (Garmin GpsMap 60Cx, Olathe, KS, USA) with European Geostationary Navigation Overlay Service (EGNOS).
ensuring accuracy of 1–1.5 m. Distances between all nests within the colony were calculated, which allowed calculations of the nearest neighbor distance (m), nest density (number of nests within the radius of 15 m), distance to the colony center (m), and distance to the center of the nest cluster (m). Colony and cluster centers were calculated as the mean coordinates of all nests within the colony and particular clusters, respectively. Nest location characteristics were described for all nests in the colony, as there was no time-gap between breeding activities of the earliest and the latest pairs of terns. All nest location characteristics were divided into separate intervals. Nest density was divided into three categories: low (≤4 nests within a radius of 15 m), intermediate (between 4 and 11 nests within a radius of 15 m), and high (≥11 nests within a radius of 15 m). Nests were grouped as near (≤1.5 m), intermediate (between 2 and 5.5 m), and far (≥5.5 m) to the nearest neighbors. Nests were also classified by distance to the colony/cluster center as central (distance to the colony center ≤70 m; distance to the cluster center ≤10 m), intermediate (distance to the colony center between 70 and 150 m; distance to the cluster center between 10 and 45 m), and edge (distance to the colony center ≥150 m; distance to the cluster center ≥45 m) nests. The intervals of all categories were established ad hoc to produce similar sample sizes. We avoided the confounding effect of clutch size on the size of eggs by investigating spatial patterns of egg size only for three-egg clutches.

Statistical Analyses.—Main-effects and factorial analysis of variance (ANOVA) were used to investigate influence of different spatial characteristics on clutch and egg size. Post-hoc analyses were performed with the Tukey HSD procedure. Significance of linear and quadratic trends among different groups of categorical variables was checked with trend analysis. All statistical procedures followed Zar (1996).

RESULTS

Nest location within the colony depended on time of breeding; pairs breeding in different periods of the season differed in distance to the cluster center and were in areas of different nest density (ANOVA: F = 2.89, df = 1, P = 0.039; F = 10.06, df = 1, P < 0.001, respectively). Nests of the earliest breeders were closer to the centers of nest clusters in comparison to nests of pairs which bred in the following 10-day period (Tukey test: P = 0.035, Fig. 2). Terns built nests in areas of highest nest density at the beginning of the breeding season and occupied less dense areas as the season progressed (trend analysis: F = 20.47, df = 1, P < 0.001). There was no relationship between timing of breeding and either nearest neighbor distance or distance to the colony center (all P > 0.15).

The mean (± SD) clutch size in the colony was 2.47 ± 0.76 eggs (n = 125). Three-egg clutches were recorded most frequently (55.2%), followed by clutches of two eggs (27.2%), and one egg (14.4%). Four-egg clutches were recorded sporadically (3.2%). Clutch size did not differ between nest clusters (ANOVA: F = 2.26, df = 3, P = 0.09). Clutch size was significantly related to the distance to cluster center and nearest neighbor distance after accounting for timing of breeding (ANOVA: F = 3.19, df = 2, P = 0.045; F = 3.36, df = 2, P = 0.038, respectively), but was not affected by the distance to the colony center (ANOVA: F = 0.38, df = 2, P = 0.69). Pairs which nested closer to the centers of clusters and closer to their nearest neighbor had significantly higher clutch size (trend analysis: F = 5.70, df = 1, P = 0.019, Fig. 3; F = 3.93; df = 1, P = 0.049, respectively).

The mean (± SD) egg length was 38.70 ± 1.54 mm, the mean breadth was 27.64 ± 0.76 mm, and the mean volume was 14.40 ± 1.05 cm³ (n = 309). We found no trade-off between egg volume and clutch size (ANOVA: F = 2.93, df = 2, P = 0.06), but there were significant differences in egg
breadth between clutch size classes (ANOVA: $F = 3.05$, $df = 2$, $P = 0.032$). Egg volume did not differ between nest clusters (ANOVA: $F = 2.02$, $df = 3$, $P = 0.13$). There was significant temporal variation in volume, breadth, and length of eggs (ANOVA: $F = 2.72$, $df = 3$, $P = 0.048$; $F = 3.53$, $df = 3$, $P = 0.033$; $F = 3.87$, $df = 3$, $P = 0.011$, respectively). There was a constant decrease in egg length over the course of the season (trend analysis: $F = 11.20$, $df = 1$, $P = 0.001$). Egg breadth and volume had no linear trends in time (trend analysis: all $P > 0.1$). Egg length and volume were related to nest density (ANOVA: $F = 3.59$, $df = 2$, $P = 0.033$; $F = 3.19$, $df = 2$, $P = 0.048$, respectively). Eggs had the highest length and volume in the intermediate nest densities (quadratic trend analysis: $F = 7.17$, $df = 1$, $P = 0.009$; $F = 6.35$, $df = 1$, $P = 0.014$, Fig. 4, respectively). There was a significant relationship between distance to the cluster center and within-clutch variation in egg volume (ANOVA: $F = 3.32$, $df = 2$, $P = 0.043$). Edge clutches had higher variation in egg volume in comparison to more central clutches (trend analysis: $F = 5.07$, $df = 1$, $P = 0.028$, Fig. 5). Similarly, within-clutch variation in egg breadth increased with increasing distance to the colony center (trend analysis: $F = 4.77$, $df = 1$, $P = 0.033$).

**DISCUSSION**

We found specific spatial patterns in establishment of the colony of Whiskered Terns at Jeziorsko Reservoir. Nest sites in the central parts of clusters were occupied earlier in comparison to the edge sites. Pairs which bred at the edges of nest clusters and distant from the nearest neighbors had smaller clutches. The mean egg size of low-density pairs was smaller in comparison to the pairs nesting in denser areas. These findings indicate that quality of Whiskered Terns breeding in the sparse peripheral zones of the nest clusters was lower in comparison to quality of pairs nesting in more central or denser areas. This was further confirmed by higher within-clutch variation in egg size recorded for edge pairs. Intra-clutch variation in egg size for the majority of studied land species was negatively correlated with fledging success and decreased with the age of parents (Sydeman and Embley 1992). The nesting habitat of Whiskered Terns was highly
homogenous and its quality across the colony did not show any significant variation. Thus, nesting in central parts of clusters could possibly offer highest advantages in terms of fitness, as it was likely to provide more efficient protection against predators and promote higher breeding success (Velando and Freire 2001). Patchy distribution of nesting habitat suggested lack of the central-periphery gradients across the entire colony. In fact, neither clutch nor egg size was affected by distance to the colony center. Instead, each nest cluster acted as a separate unit, in which central-periphery gradients of clutch and egg size occurred.

Most studied larid species were found to follow the central-periphery model of nest distribution. Higher reproductive success of pairs breeding in the center of colonies has been reported for Black-headed Gull (Chroicocephalus ridibundus) (Patterson 1965), Black-legged Kittiwake (Rissa tridactyla) (Coulson 1968a), Ring-billed Gull (Larus delawarensis) (Dexheimer and Southern 1974), and Caspian Tern (Hydroprogne caspia) (Antolos et al. 2006). Spatial patterns within the colonies of other larids were more complicated and could not be unequivocally assigned to any of the suggested theoretical models. For example, Common Tern (Sterna hirundo) breeding success was positively correlated with nest density, but negatively affected by nearest neighbor distance (Becker 1995).

The highest egg volume of Whiskered Terns was in the intermediate nest densities. Lower egg volume of pairs breeding in the most densely occupied areas suggests highest nest densities are not favored by high-quality pairs of Whiskered Terns. Nesting in particularly high densities by several species of larids was disadvantageous in terms of fitness. Negative relationships of reproductive success with nest density were generally related to intraspecific aggression. Birds nesting in high-density areas are likely to be engaged in more bouts of agonistic behavior than individuals breeding in more sparse areas of a colony (Butler and Trivelpiece 1981). Thus, high-density pairs are likely to devote more time to nest defense and invest less in the other parental activities such as food provisioning. It is also possible that chicks raised in high nest density areas under conditions of food shortage may easily enter territories of others and be attacked by conspecific adults (Hunt and McLoon 1975). Decreased chick survival rates in the high-density parts of colonies have been recorded for some larids, including European Herring Gull (Larus argentatus) (Parsons 1975) and Glaucous-winged Gull (L. glaucescens) (Hunt and Hunt 1976). A positive relationship between egg losses and nearest neighbor distance was found for Kelp Gull (L. dominicanus) (Fordham 1964) and fledgling success of the Great Black-backed Gull (L. marinus) was lowest in the high-density pairs (Butler and Trivelpiece 1981). These findings support the hypothesis that there could be a trade-off between the need for protection against predators and avoidance of intraspecific aggression in some colonial larid species (Hunt and Hunt 1976).

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**LITERATURE CITED**


NEST-SITE SELECTION AND NESTING SUCCESS OF GREY-BACKED THRUSHES IN NORTHEAST CHINA

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ABSTRACT.—We identified microhabitat features affecting nest-site selection and examined nest-site characteristics associated with success for the Grey-backed Thrush (Turdus hortulorum) in the Dagang Forestry Farm, Jilin Province, northeast China. We collected data from 79 nests from April to August 2008. Twenty-nine nests (36.7%) were successful, 47 (59.5%) failed due to predation, and the rest were either destroyed by storms or abandoned. The overall daily survival rate (DSR) was 0.9563 ± 0.0072. Nest attempts beginning late in the breeding season were more likely to be depredated. Averaged DSR of laying and late nesting (days 7-12 after hatching) periods was higher than those of incubation and brooding (days 1-6 after hatching). We compared habitat variables between nest and random sites and assessed the effects of nest-location and nest-patch characteristics on DSR. Grey-backed Thrushes selected nest sites with shorter ground cover and a high density of small trees and shrubs. DSR was positively related to distance from the nest to the main stem of the nest tree and negatively correlated with horizontal exposure. Further research should focus on identification of nest predators, implications of nest exposure and begging calls on nestling success, and breeding habitat requirements at different spatial and temporal scales of Grey-backed Thrush in fragmented landscapes of northeast China. Received 7 July 2010. Accepted 4 March 2011.

Nest-site selection is a critical aspect of reproductive success for birds because species select different nest sites to alleviate inter- and intra-specific competition (Cody 1981), and decrease the probability of predation (Joern and Jackson 1983). Nest-site selection probably affects individual fitness, and population dynamics (Roth and Johnson 1993, Aguilar et al. 2008). Predation has been recognized as a primary cause of nest failure among forest-nesting passerines (Ricklefs 1969), and investigating the relationship between nest-site characteristics and nest predation has become a focus in ornithology (Martin and Roper 1988, Hoover and Brittingham 1998, Aguilar et al. 2008).

Habitat characteristics, including canopy height and closure, average height of shrubs, number of trees, diversity of plant species, ground cover, elevation, and vegetation layers are considered by birds during the decision-making processes of nest-site selection (Hoover and Brittingham 1998, Briskie et al. 1999, Gjerdrum et al. 2005, Aguilar et al. 2008). Many studies have examined the relationship between nesting success and habitat features, including nest exposure or concealment (Hatchwell et al. 1996, Johnson 1997), ground cover (Bertin 1977), vegetation density around nests (Kellerher and O’Halloran 2007), proximity to forest edges (Driscoll et al. 2005, Kaiser and Lindell 2007), and size of forest fragments (Fauth 2000).

Nest-site selection, niche partitioning, population dynamics, and nest predation have been studied for many species of Turdidae, including Song Thrush (Turdus philomelos) (Paradis et al. 2000, Kellerher and O’Halloran 2007), Common Blackbird (T. merula) (Paradis et al. 2000), and Wood Thrush (Hylocichla mustelina) (James et al. 1984, Roth and Johnson 1993, Hoover and Brittingham 1998, Farnsworth and Simons 2000, Newell and Kostalos 2007). The Grey-backed Thrush (Turdus hortulorum), among the many Turdidae species, has received little attention, although this is an abundant species with a wide distribution. The breeding range of this species includes northeastern China, southeast Russian Siberia, and North Korea and they overwinter in southeastern China and northern Vietnam, occasionally passing through Japan and Taiwan (Cheng et al. 1995, Collar 2005).

Little is currently known about nest-site selection and characteristics important for success of Grey-backed Thrush. Most foraging occurs on the ground by scratching in the leaf litter, and this species feeds on insects and fruits. Previous work describes nests in shrubs and trees (Zhao 1982, Collar 2005). This species inhabits mainly open deciduous forests and dense broadleaf evergreen forests on low mountains and hills up to 1,100 m (Yang and Tian 1987, Cheng et al. 1995, Collar...
2005), and rarely occupies small patches and forest edges (Deng et al. 2003, Deng and Gao 2005b). Global population size and trends have not been quantified, and the status of 'Least Concern' was assigned by Birdlife International (Birdlife International 2009) and IUCN. More detailed knowledge of the nesting ecology of the Grey-backed Thrush would increase our understanding of the life history and breeding ecology of this species.

We examined nesting habitat to empirically understand factors influencing nest-site selection and nesting success of Grey-backed Thrush at two scales, including nest-location (characteristics within the immediate vicinity of the nest) and nest-patch (characteristics of the habitat surrounding the nest) (Martin and Roper 1988, Siepielski et al. 2001). Our objectives were to: (1) compare characteristics of Grey-backed Thrush nest sites to available habitats at the nest-patch scale, and (2) identify habitat attributes and nest-location characteristics (i.e., nest height, nest exposure) associated with nesting success.

METHODS

Study Area.—This study was conducted in the Dagang Forestry Farm (43° 34’-41’ N, 126° 03’-14’ E), an area of ~12,000 ha of natural secondary forest fragmented by farmlands and scattered plantations in Jilin Province, China, from April to August 2008. The forestry farm extends from the eastern slope of the Changbai Mountains to the western edge of the Song-Liao plains (the northeastern plain of China). Conifer (Larix spp.) plantations are managed for timber extraction. All secondary forests are protected by the government, but unlawful forest thinning occasionally occurs. This region is in the temperate zone, and has a continental monsoon climate characterized by a cold (coldest in Jan with average temperature of -18 to -20°C) and snowy winter, a windy spring and autumn, a hot summer (average temperature of 21-23°C) and humid summer (summer average rainfall = 434 mm), and only a short frost-free period (130-140 days) (Li 2007).

Four plots were established with areas of ~10, 19, 38, and 54 ha, respectively, at least 500 m apart, and with an elevation range of 328 to 477 m. These plots were mainly covered by homogenous secondary deciduous forest of 50 to 60 years of age adjacent to farmlands and a few plantations. The dominant trees included Mongolian oak (Quercus mongolica), Pierot willow (Salix pierotii), Dahurian birch (Betula dahurica), Manchurian walnut (Juglans mandshurica), large leaf Chinese ash (Fraxinus rhynchophylla), and Japanese elm (Ulmus japonica), Manchurian Schneider's buckthorn (Rhamnus schneideri), Chinese hawthorn (Crataegus pinnatifida), Amur Maple (Acer ginnala), Amur honeysuckle (Lonicera maackii), and Manchurian lilac (Syringa reticulata) occupied the shrub layer in the study area. Narrow-leaved and broad-leaved herbaceous plants were the dominant life forms of ground cover.

No regulations forbid human use of forests in the Dagang Forestry Farm, and economic activities include cultivating maize and rice around the forest, raising and harvesting forest frogs in the forest, and grazing cattle. Some unpaved paths (> 2 m wide) have been created because of vehicular traffic related to grazing and farming.

Data Collection.—We systematically walked transect lines ~8 m apart to search for nests of Grey-backed Thrushes within the plots from late April to early July 2008, and recorded the number of eggs or nestlings in each nest and whether it was successful or not. We revisited the nests every 2-3 days. We conducted daily checks of nests in which nestlings were about to fledge and nests with eggs (or nestlings) that disappeared or failed to hatch on the expected day. Nests were considered successful when the nestlings (at least 1) disappeared at the expected time of fledging (±1 day). We considered nests to have failed when eggs disappeared, nests were demolished, or nestlings were absent before their expected fledging date (Hoover and Brittingham 1998, Aguilar et al. 2008).

We collected vegetation data at each nest site during July and early August. Nest-site characteristics, including nest-location and nest-patch data, were measured in a 0.04-ha circle (11.3-m radius) centered on the nest, using a modified version of Noon (1981), as described by Chu and Zheng (1993). Diameter at breast height (DBH) of the nest tree was recorded as well as nest height (m), distance from the nest to the main stem of the nest tree (cm), and exposure (%) for each nest location (Table 1).

The exposure of each nest was evaluated with a modified version of a method described by Hoover and Brittingham (1998). We painted 10 red circles 5 cm in diameter, 6 cm apart from each other, in two rows of five on a white cover board. The cover board was placed directly facing east, south, west, and north, respectively to calculate...
TABLE 1. Nest-location and nest-patch variables included in the analyses of Grey-backed Thrushes in Dagang Forestry Farm, China, in 2008.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest-location</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest-tree DBH</td>
<td>Diameter at breast height of the vegetation supporting the nest, averaged for vegetation with multiple stems</td>
<td>Benin 1977</td>
</tr>
<tr>
<td>Nest height</td>
<td>Distance between the ground and the upper margin of nest</td>
<td>Förchler and Kalko 2006</td>
</tr>
<tr>
<td>Distance from nest to main stem</td>
<td>Distance between the center of nest and the main stem of nest tree</td>
<td>Hoover and Brittingham 1988</td>
</tr>
<tr>
<td>Horizontal exposure</td>
<td>Visibility of the nest in a horizontal plane at nest height</td>
<td>Martin and Roper 1988</td>
</tr>
<tr>
<td>Vertical exposure</td>
<td>Visibility of the nest in a vertical plane</td>
<td>Götmark et al. 1995</td>
</tr>
<tr>
<td>Total exposure</td>
<td>Combination of vertical and horizontal exposure</td>
<td>Hatchwell et al. 1996</td>
</tr>
<tr>
<td>Nest-patch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to edge</td>
<td>Distance of the nest to the nearest external edge</td>
<td>Johnson 1997</td>
</tr>
<tr>
<td>Distance to path</td>
<td>Distance of the nest to the closest path (≥ 2 m wide)</td>
<td>Driscoll et al. 2005, Newell and Kostalos 2007, Miller et al. 1998</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>Percentage of the forest floor covered by vertical projection of tree (≥ 5 m) crowns</td>
<td>Sargent et al. 2003</td>
</tr>
<tr>
<td>Ground cover</td>
<td>Proportion of the forest floor covered by herbs between 0 and 0.5 m</td>
<td>Bertin 1977</td>
</tr>
<tr>
<td>Height of ground cover</td>
<td>Average of 10 random measurements of height of grasses in the 0.04-ha circle</td>
<td>Eiserer 1980</td>
</tr>
<tr>
<td>Density of shrubs</td>
<td>Density of main stems of shrubs below breast height along two arm-length perpendicular transects (≥ 2 m wide) that bisected the 0.04-ha circle</td>
<td>Yang and Tian 1987</td>
</tr>
<tr>
<td>Basal area of small trees</td>
<td>Total area calculated from DBH of all the standing trees (3 cm ≤ DBH &lt; 8 cm)</td>
<td>Driscoll et al. 2005</td>
</tr>
<tr>
<td>Basal area of large trees</td>
<td>Total area calculated from DBH of all the standing trees (DBH ≥ 8 cm)</td>
<td>Kelleher and O’Halloran 2007</td>
</tr>
</tbody>
</table>

The horizontal exposure. The number of circles more than half-visible from each direction at a lateral distance of 3 m (at nest height) was recorded. The exposure value of each nest was computed by summing the number of circles from the four lateral directions and dividing by 40. The horizontal exposure was ranked as one if the value was between 0 and 20% (including 20%), then two, three, four, or five, for percent exposure increasing by 20% increments. Total exposure equaled the sum of horizontal and vertical exposure. For example, total exposure of a nest would be 11 when its horizontal, upper and ground-level exposure was two, five, and four, respectively. Nests with values closer to 15 had greater exposure to predators.

Vertical exposure was divided into upper and ground-level exposure. The 1-m² area over the nest was the core area for shading relative to the small averaged area of each nest (0.0117 m²). The upper exposure was estimated as the percent exposure between 0 and 0.5 m above the ground within a radius of 3 m centered on each nest. The upper and ground-level exposure was ranked as one if the percent exposure was between 0 and 20% (including 20%), then two, three, four, or five, for percent exposure increasing by 20% increments. Total exposure equaled the sum of horizontal and vertical exposure. For example, total exposure of a nest would be 11 when its horizontal, upper and ground-level exposure was two, five, and four, respectively. Nests with values closer to 15 had greater exposure to predators.

Distance to the closest path and forest edge (most have forest-farmland edge with few forest-forest opening edge) was measured by pacing, and recorded as 150 m if > 150 m. We measured the following nest-patch variables within a 0.04-ha circular plot centered on the nest directly: canopy
TABLE 2. Spearman’s correlation matrix for variables included in models for nest-site selection of Grey-backed Thrushes in Dagang Forestry Farm, China, in 2008.

<table>
<thead>
<tr>
<th>Distance to edge</th>
<th>Distance to path</th>
<th>Canopy cover</th>
<th>Ground cover</th>
<th>Height of ground cover</th>
<th>Density of shrubs</th>
<th>Basal area of small trees</th>
<th>Basal area of large trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to path</td>
<td>0.090</td>
<td>0.312**</td>
<td>-0.241**</td>
<td>-0.013</td>
<td>-0.017</td>
<td>-0.279**</td>
<td>0.470**</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>1.000</td>
<td>0.136</td>
<td>-0.079</td>
<td>-0.147</td>
<td>0.097</td>
<td>0.163*</td>
<td>0.245*</td>
</tr>
<tr>
<td>Ground cover</td>
<td>1.000</td>
<td>0.363**</td>
<td>-0.332**</td>
<td>-0.252*</td>
<td>-0.321**</td>
<td>-0.100</td>
<td>-0.064</td>
</tr>
<tr>
<td>Height of ground cover</td>
<td>1.000</td>
<td>-0.237**</td>
<td>1.000</td>
<td>0.292**</td>
<td>-0.316**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area of small trees</td>
<td>1.000</td>
<td>-0.237**</td>
<td>1.000</td>
<td>0.292**</td>
<td>-0.316**</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Correlation significant at the 0.05 level (2-tailed).
** Correlation significant at the 0.01 level (2-tailed).

cover (Bibby et al. 2000), ground cover, and height of ground cover. Species, height, and DBH of trees (DBH ≥ 3.0 cm), and number of shrub main stems were measured, and transformed to the remaining nest-patch variables, including density of shrubs, basal area of small trees (3 cm ≤ DBH < 8 cm), and large trees (DBH ≥ 8 cm). Basal area was calculated with the equation: Basal area = \( \sum \pi (DBH/2)^2 \). All variables selected were based on studies of nest-site selection for other species of Turdidae (Table 1).

We used a random numbers table to select one random plot by pacing for comparison against the nest-patch data from the cardinal directions of east, south, west, and north, which were ~50 m from the nests (Martin and Roper 1988). The random plots had the same shape and area as nest-site plots. We measured the same nest-patch characteristics in the random plots as in the nest-site plots.

Data Analyses.—We estimated daily survival rate (DSR) of Grey-backed Thrushes using Program MARK Version 6.1 (White and Burnham 1999, Cooch and White 2010). We evaluated the variation of DSR across the entire breeding season by building a trend model, reflecting the relationship between DSR and the increasing days of the breeding season. We assumed a complete nesting cycle of 29 days including four periods: laying (5 days), incubation (12 days), brooding (days 1–6 after hatching), and late nestling (days 7–12 after hatching). We estimated the DSR of each nest age, and compared them among different nestling periods.

We used original data for the analyses of nest-site selection. We compared habitat characteristics of nest sites and random plots by binomial logistic regression with used or unused (1 or 0) as the categorical dependent variable. Continuous explanatory variables were distance to edge, distance to path, canopy cover, ground cover, height of ground cover, density of shrubs, basal area of small trees, and basal area of large trees. Correlations among variables could compromise the results of multiple regressions. However, Spearman’s correlation matrix for variables included in nest-site selection models did not indicate strong correlation \( (r > 0.6 \text{ and } P < 0.05; \text{Hosmer and Lemeshow 1989}) \) between any two explanatory variables (Table 2). Thus, we did not analyze the effects of interactions among variables on nest-site selection.

The best subset of models was selected from all possible combinations using Akaike’s Information Criterion (AIC) to evaluate the relative effect of different habitat variables on nest-site selection. The AICc (second-order Akaike’s Information Criterion for small sample sizes), \( \Delta \text{AIC}_c \) (the difference in AICc between each candidate model and the model with the lowest \( \text{AIC}_c \)), and Akaike weights \( (W) \) were used to rank the models. We also conducted goodness-of-fit tests on all models using a log-likelihood ratio \( \chi^2 \) statistic to assess their closeness of fit. Relative importance of each variable was assessed by sum of model weights containing the variable (Burnham and Anderson 2002).

We incorporated six nest-location and eight nest-patch habitat variables between successful and depredated nests to evaluate the effects of nest-site habitat characteristics on nesting success. We screened variables by significance tests (Independent-sample t-tests for normally distributed data and Mann-Whitney U-tests for abnormally distributed data) to increase the statistical power under the circumstance of relative small sample size, and included variables when they had significant differences at the 0.25 level but did not correlate with each other strongly \( (r > 0.6 \text{ and } P < 0.05) \). Models comprised of intercept and...
selected variables were built by Program MARK, and ranked by AIC_c and W_i. All statistical analyses were performed with STATISTICA Version 8.0 (StatSoft Inc. 2007); values are presented as means ± SE.

RESULTS

Seventy-nine nests of Grey-backed Thrush were found in the plots. Fifteen of the 79 nests were excluded from DSR analysis because of predation (cracked egg shells in the nests and/or on the ground) (12 nests), abandoned after extended incubation (2 nests), and destroyed during a storm (1 nest). All 79 nests were included in analyses of nest-site selection, but only 64 nests were included in estimation of DSR.

Overall DSR, irrespective of the variation among nests and all dates, was 0.9563 ± 0.0072 (effective sample size based on exposure days = 760). The apparent nesting success based on the overall constant DSR was 0.274 (0.9563 ^ 0.9563). DSR of Grey-backed Thrushes decreased during the 88-day nesting season, according to the trend model: $DSR = 1/(1 + exp (-3.2049040 + 0.0042267*t))$ (where t refers to the day in the nesting season). DSR of each nest age was estimated, and averaged DSR of laying (0.9581 ± 0.0009) and late nestling (0.9580 ± 0.0027) periods were higher than those of incubation (0.9561 ± 0.0021) and brooding (0.9558 ± 0.0021) periods (Fig. 1). However, no significant differences were detected between nestling periods ($F = 1.955, P = 0.147$).

![Daily survival rate (DSR) for each nest age of Grey-backed Thrushes in Dagang Forestry Farm, China, in 2008.](image)

Nest-site Characteristics.—Nests were built in 15 plant species, including eight tree and seven shrub species. Forty of the 79 nests (51.9%) were in shrubs, 32 (40.5%) were in trees, and six (7.6%) were on stumps remaining after logging events (average height of stumps was 1.27 ± 0.49 m). Among nests in shrubs, 17.7 and 16.5% were in Manchurian Schneider buckthorn and Chinese hawthorn, respectively. The predominant trees used for nesting included Japanese elm (11.4%), Ussurian pear (Pyrus ussuriensis) (10.1%), and Dahurian birch (10.1%). Mongolian Scotch pine (Pinus sylvestris L. var. mongolica Litvin) was the only evergreen tree used.

Sixty-nine of 79 (87.3%) nest trees had DBH equal to or >3.0 cm. Tree species with DBH ≥ 3.0 cm and their relative abundance at nest sites (5,442 trees) and random plots (4,520 trees), respectively, was calculated and total density of trees at nest sites (1,722/ha) was higher than in random plots (1,430/ha). Species composition and their relative abundances were similar between nest sites and random plots (Fig. 2). Grey-backed Thrushes preferred Manchurian Schneider buckthorn, Chinese hawthorn, Manchurian lilac, Amur honeysuckle, Japanese elm, Manchurian pear, and Dahurian birch as nesting trees, and did not select bird cherry (Padus racemosa), Mandshurian lilac (Tilia mandshurica), large leaf Chinese ash, Mongolian oak, and Amur cork-tree (Phellodendron amurense), which accounted for 33.6% of the total trees (Fig. 2).
Significance tests indicated the average density of shrubs at nest sites (1.21 ± 0.46 individuals/m²) was significantly higher than at random plots (0.95 ± 0.42 individuals/m²), and basal area of small trees at nest sites (2.24 ± 0.78 m²/ha) was also greater than at random plots (1.64 ± 0.88 m²/ha) (Table 3). The average height of large and small trees was 8.97 ± 1.53 m and 4.33 ± 0.56 m, respectively. The correlation matrix indicated density of shrubs was negatively correlated with ground cover ($r_s = -0.332, P = 0.001$) and height of ground cover ($r_s = -0.237, P = 0.003$) (Table 2).

A set of four candidate models whose $\Delta$AIC$_c$ were $<2$ were selected from the potential models (Table 4), and we compared them with the global model (Model 1, Table 4; all variables included) and null model (Model 2, Table 4; no variables). We used $P < 0.05$ to indicate a good model when testing for the fitness of a model with log-likelihood ratio tests. All models except null model were potentially good ($P < 0.001$), including the global model. The model building procedures indicated Model 3 with the highest $W_i$ of 0.325 was the best model. The global model only had a $W_i$ of 0.004 (Table 4).

Height of ground cover, density of shrubs, and basal area of small trees were included in the best model with the relative importance of 0.599, 1.000, and 1.000, respectively. Density of shrubs ($P = 0.027$) and basal area of small trees ($P = 0.012$) were also significant in the models based on Wald statistics, but height of ground cover was not ($P = 0.134$). The relative importance of other variables excluded from the best model was 0.004, except that distance to edge accounted for the importance of 0.444. Grey-backed Thrushes built nests in areas with a lower height of ground cover, and a higher density of small trees and shrubs.

Successful and Depredated Nests.—The distance from nest to main stem and horizontal exposure at the nest-location scale, and density of shrubs at the nest-patch scale met the criteria of variable selection ($P \leq 0.25$), respectively, and correlation analyses did not indicate a strong correlation among them. Distance from the nest to the main stem of the nest tree was the only significant variable associated with nesting success at the 0.05 level.

Model 3 met the needs of model fit and parameter parsimony, and was the best with the highest $W_i$ of 0.202 (Table 5). Distance from nest to main stem and horizontal exposure were included in the best model with relative importance of 0.647 and 0.509, respectively. Density of shrubs was not included in the best model, although its relative importance reached 0.644. Nests with closer proximity to the main stem of the nest tree and higher horizontal concealment were more likely to be successful.

There were some indications that nest exposure was associated with predation for Grey-backed Thrushes. Forty-two nests had high levels of exposure (≥ 4) with at least one of the three exposure indices (upper, ground-level, or hori-
TABLE 3. Habitat measurements (mean ± SE) at nest sites and random plots, and successful and depredated nest sites for Grey-backed Thrushes in Dagang Forestry Farm, China, in 2008. Significance tests were conducted between nest sites and random plots, and successful and depredated nest sites.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Nest sites (n = 79)</th>
<th>Random plots (n = 79)</th>
<th>Successful (n = 29)</th>
<th>Depredated (n = 35)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest-location</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest-tree DBH (cm)</td>
<td>8.70 ± 5.47</td>
<td>8.44 ± 4.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest height (m)</td>
<td>1.93 ± 1.05</td>
<td>1.89 ± 0.55</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from nest to main stem (cm)</td>
<td>8.31 ± 17.65*</td>
<td>25.54 ± 30.66*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horizontal exposure</td>
<td>3.21 ± 0.89*</td>
<td>3.46 ± 0.76*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical exposure</td>
<td>4.03 ± 1.85</td>
<td>3.89 ± 1.52</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total exposure</td>
<td>7.24 ± 2.37</td>
<td>7.34 ± 1.88</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest-patch</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to edge (m)</td>
<td>66.73 ± 54.23</td>
<td>74.03 ± 56.18</td>
<td>70.83 ± 55.36</td>
<td>56.60 ± 39.33</td>
</tr>
<tr>
<td>Distance to path (m)</td>
<td>18.33 ± 23.31*</td>
<td>24.00 ± 21.42*</td>
<td>20.76 ± 27.59</td>
<td>16.23 ± 14.00</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>83.76 ± 12.42</td>
<td>80.63 ± 16.92</td>
<td>85.17 ± 11.48</td>
<td>82.49 ± 10.27</td>
</tr>
<tr>
<td>Vertical exposure</td>
<td>8.70 ± 5.47</td>
<td>8.44 ± 4.73</td>
<td>8.31 ± 17.65*</td>
<td>25.54 ± 30.66*</td>
</tr>
<tr>
<td>Total exposure</td>
<td>7.24 ± 2.37</td>
<td>7.34 ± 1.88</td>
<td>7.03 ± 2.31</td>
<td>6.89 ± 1.52</td>
</tr>
<tr>
<td>Vertical exposure</td>
<td>4.03 ± 1.85</td>
<td>3.89 ± 1.52</td>
<td>3.75 ± 1.26</td>
<td>3.63 ± 1.17</td>
</tr>
<tr>
<td>Total exposure</td>
<td>7.24 ± 2.37</td>
<td>7.34 ± 1.88</td>
<td>7.03 ± 2.31</td>
<td>6.89 ± 1.52</td>
</tr>
</tbody>
</table>

* P < 0.05 (comparison between successful and depredated nests).  
** P < 0.01.

 horizontal exposure); of these, 33% (n = 14) were successful. However, among the 34 residual nests whose three exposure indexes were low (≤ 3), 44% (n = 15) succeeded.

**DISCUSSION**

*Nest-site Characteristics.*—Grey-backed Thrushes nested in areas with lower ground cover and a higher density of small trees and shrubs. Other researchers have found that shrub-nesting birds, such as Wood Thrush and Song Thrush (Hoover and Brittingham 1998, Kelleher and O’Halloran 2007), build nests in areas with higher shrub densities. Our results were consistent with their findings (Table 2). Dense shrubs may reduce the risk of predation (Joeorn and Jackson 1983, Martin 1993), and provide shade to protect nestlings from inclement weather (Weidinger 2009).

**TABLE 4.** Model selection for predicting nest-site selection by Grey-backed Thrushes in Dagang Forestry Farm, China, in 2008. Models were ranked according to AIC. −2log(l) referred to −2log-likelihood. All models used n = 158 sampling plots.

<table>
<thead>
<tr>
<th>ID</th>
<th>Predictors</th>
<th>−2log(l)</th>
<th>K</th>
<th>ΔAIC*</th>
<th>Wj</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Distance to edge + distance to path + canopy cover + ground cover + height of ground cover + density of shrubs + basal area of small trees + basal area of large trees</td>
<td>206.17</td>
<td>9</td>
<td>8.92</td>
<td>0.004</td>
</tr>
<tr>
<td>2</td>
<td>Null model (only intercept)</td>
<td>221.06</td>
<td>1</td>
<td>23.82</td>
<td>0.000</td>
</tr>
<tr>
<td>3</td>
<td>Height of ground cover + density of shrubs + basal area of small trees</td>
<td>197.25</td>
<td>4</td>
<td>0.00</td>
<td>0.325</td>
</tr>
<tr>
<td>4</td>
<td>Distance to path + height of ground cover + density of shrubs + basal area of small trees</td>
<td>197.61</td>
<td>5</td>
<td>0.37</td>
<td>0.270</td>
</tr>
<tr>
<td>5</td>
<td>Density of shrubs + basal area of small trees</td>
<td>197.92</td>
<td>3</td>
<td>0.68</td>
<td>0.231</td>
</tr>
<tr>
<td>6</td>
<td>Distance to path + density of shrubs + basal area of small trees</td>
<td>198.54</td>
<td>4</td>
<td>1.30</td>
<td>0.170</td>
</tr>
</tbody>
</table>

*The lowest AIC* value for this analysis was 197.25.
TABLE 5. Model selection for variation of daily survival rate of Grey-backed Thrushes incorporating nest-location and nest-patch characteristics in Dagang Forestry Farm, China, in 2008. Models were ranked according to AIC$_c$. $-2\log(l)$ referred to $-2\log$-likelihood. All models used $n = 64$ nests.

<table>
<thead>
<tr>
<th>ID</th>
<th>Predictors</th>
<th>$-2\log(l)$</th>
<th>$K$</th>
<th>AIC$_c^a$</th>
<th>$w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Distance from nest to main stem + horizontal exposure + density of shrubs</td>
<td>201.24</td>
<td>4</td>
<td>0.16</td>
<td>0.186</td>
</tr>
<tr>
<td>2</td>
<td>Null model (only intercept)</td>
<td>209.95</td>
<td>1</td>
<td>2.83</td>
<td>0.049</td>
</tr>
<tr>
<td>3</td>
<td>Distance from nest to main stem + horizontal exposure</td>
<td>203.10</td>
<td>3</td>
<td>0.00</td>
<td>0.202</td>
</tr>
<tr>
<td>4</td>
<td>Density of shrubs</td>
<td>205.30</td>
<td>2</td>
<td>0.19</td>
<td>0.184</td>
</tr>
<tr>
<td>5</td>
<td>Distance from nest to main stem + density of shrubs</td>
<td>203.65</td>
<td>3</td>
<td>0.55</td>
<td>0.154</td>
</tr>
<tr>
<td>6</td>
<td>Horizontal exposure + density of shrubs</td>
<td>203.65</td>
<td>3</td>
<td>1.03</td>
<td>0.120</td>
</tr>
<tr>
<td>7</td>
<td>Distance from nest to main stem</td>
<td>206.43</td>
<td>2</td>
<td>1.32</td>
<td>0.105</td>
</tr>
</tbody>
</table>

* The lowest AIC$_c$ value for this analysis was 209.33.

Grey-backed Thrushes preferred species of shrub such as Manchurian Schneider buckthorn and Chinese hawthorn, whose umbrella-like crowns increased coverage over nests and aided in concealment. High density of small trees may have been important for shading and concealing nests, preventing potential visually oriented aerial predators, such as Eurasian Jay (Garrulus glandarius), owls, and woodpeckers from discovering the nests (Weidinger 2009).

Eiserer (1980) found that American Robins (T. migratorius) preferred to forage in short grass because of a lower predator attack rate, greater ease of locomotion, and hunting efficiency. Tall grass may make foraging difficult when Grey-backed Thrushes forage in the leaf litter layer around the nest. Thus, they tended to nest in areas with less short ground cover although shorter grass may increase their exposure to predators. They preferred areas with shorter grass, and chose areas with dense shrubs to compensate for the high exposure from shorter ground cover. High-density shrubs might inhibit growth of herbs on the ground based on their negative correlations (Table 2). We believe Grey-backed Thrushes probably make trade-offs between height of ground cover and density of shrubs.

Successful Nests Versus Depredated Nests.—Nearly 60% of nests of Grey-backed Thrushes were depredated and nest predation is a major cause of nest failure for forest passerines (Ricklefs 1969). Successful nests were constructed relatively close to the main stems of trees and shrubs, and also tended to be more concealed horizontally.

We agree with other researchers that nesting close to the main stem provided strong support to the nest structure (Delannoy and Tossas 2002, Sargent et al. 2003). We speculate nests near the main stem may also decrease the upper exposure to predators based on preference of thrushes for nest trees with umbrella-like crowns.

Predation rates were lower at nests with more dense foliage around the nest and least exposure in 29 of 36 studies, including both grassland/marsh and shrub/woodland habitats and across a diversity of species (Martin 1992). The impacts of horizontal exposure were embodied in the best model of DSR for Grey-backed Thrushes that incorporated habitat characteristics. We believe high visual exposure on a single side (upper, ground-level, or horizontal) resulted in high exposure and predation risk to the nest, regardless of the amount of concealment offered on the remaining sides.

We preliminarily identified the seasonal pattern of nesting success of Grey-backed Thrushes, i.e., nest attempts late in the breeding season are more likely to be depredated. High levels of predation occurred during the incubation and brooding periods for Grey-backed Thrushes, which differs from Wood Thrushes. Anders et al. (1997) calculated DSR of Wood Thrushes in southern Missouri in 1994-1995, and found the DSR of the incubation period was highest among the four nesting periods. However, both Wood and Grey-backed thrushes had the lowest DSR in the brooding period. Begging calls and increasing visits by adults possibly exposed the nests to predators (Briskie et al. 1999). The specific factors influencing DSR dependent on year, breeding season, and nest periods needs further studies.

Gates and Gysel (1978) suggested forest edge is an ‘ecological trap’ that concentrates nests, and may increase nest predation. Flaspohler et al. (2001) reported Mayfield nest success was greater in the interior of large, closed-canopy hardwood
CONSERVATION IMPLICATIONS

Unlawful logging of large trees has decreased sharply because of conservation efforts by the government in recent years. However, farmers still cut shrubs and small trees for fuel, fences, and feed for livestock. Shrub and small trees in secondary forests should be protected, and cutting banned. Our results suggest Grey-backed Thrushes tend to nest in forests with dense shrubs and small trees. Thus, management for this species should focus on decreasing unlawful cutting of shrubs and small trees. Further studies of breeding habitat requirements at different spatial and temporal scales are needed for management and conservation of Grey-backed Thrush. In addition, major nest predators need to be identified. The implications of nestling exposure and begging calls on nestling success should be the main focus of future study.

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NESTING SUCCESS OF NEOTROPICAL THRUSHES IN COFFEE AND PASTURE

CATHERINE A. LINDELL,1,2,5 RYAN S. O’CONNOR,1,3 AND EMILY B. COHEN1,4

ABSTRACT.—We monitored nesting attempts of White-throated (Turdus assimilis) and Clay-colored thrushes (T. grayi) over 4 years in southern Costa Rica to compare nest success in recently abandoned coffee (Coffea spp.) plantations, pasture, and along roads. Daily mortality rates of Clay-colored Thrush nests were lower in pasture (0.054 ± 0.014) than abandoned coffee plantations (0.096 ± 0.012). Daily mortality rates of White-throated Thrush nests were not influenced by land-cover type but were lower at highly concealed nests (0.058 ± 0.005) compared to less concealed nests (0.090 ± 0.017), and at nests that were on the ground (0.0580 ± 0.005) versus in vegetation (0.076 ± 0.007). Daily mortality rates for nests of both species were very low at an active coffee plantation where nests were monitored in 1 year (0.006 ± 0.004 and 0.015 ± 0.015, for White-throated and Clay-colored thrushes, respectively). Nests at the active plantation were heavily concealed which, along with results for White-throated Thrushes in abandoned coffee, indicates concealment has a strong influence on tropical thrush nest success. Nest success appears to be heavily dependent on factors that may influence both concealment and or habitat for predators. Nest success also appears to be strongly site-specific, making it difficult to provide general statements about the conservation value of different land-cover types. Received 22 September 2010. Accepted 9 February 2011.

An estimated 50% of what was once tropical forest has been cleared (Wright 2005). The agricultural land-cover types that replace tropical forest will influence future population sizes and fates of numerous species (Vandermeer and Perfecto 2007). Some land-cover types are considered of greater conservation value than others, usually on the basis of relative abundance and or presence/absence data (e.g., Sodhi et al. 2005). For example, more bird species have been detected in rustic coffee (Coffee spp.) plantations (those with shade trees) than pastures (Petit and Petit 2003, Estrada and Coates-Estrada 2005), suggesting that coffee plantations are of higher conservation value.

Successful nesting is arguably a much more important indicator of conservation value than presence of a species in a land-cover type, but information on reproductive success of tropical birds in different land covers is sparse (e.g., Gleffe et al. 2006, Sekercioglu et al. 2007). Coffee and pasture cover vast areas of the Neotropics (Fearnside 1993, Rice and Ward 1996), but no studies have quantitatively compared nest success in coffee and pasture.

Clay-colored Thrushes (Turdus grayi) tend to use open habitats such as gardens and pastures with some trees, although they also use forest during the non-nesting season. Bulky, cup nests are built on and above the ground in locations hidden by foliage or in banks (Stiles and Skutch 1989, Lindell and Smith 2003). White-throated Thrushes (T. assimilis) forage and nest in both forest and non-forest habitats, on and above the ground (Cohen and Lindell 2004, Sekercioglu et al. 2007). Despite their apparent ability to use non-forest land-cover types, regional forest cover loss in Costa Rica in the last century may have contributed to a reduced country-wide distribution of the White-throated Thrush (Stiles and Skutch 1989, Cohen and Lindell 2005). Their nests are similar in structure to those of the Clay-colored Thrush.

Previous work suggested higher daily mortality rates for nests of Clay-colored and White-throated thrushes in coffee compared to pasture (Lindell and Smith 2003), although sample sizes were small. Thus, based on nest success, coffee plantations may be of lower value than pastures for these species.

Our first objective was to test the prediction that nest success of Clay-colored and White-throated thrushes would be greater in pasture than coffee. We discovered during field work that both species also nested in road banks and included road banks as a third land-cover type. A few White-throated Thrush nests were found in forest fragments and this was a fourth land-cover type for this species. Our second objective was to...
investigate influences besides land-cover type on
nest success. We documented nest site character¬
istics that made nesting attempts more or less
likely to fail by identifying sources of variation in
nest success (e.g., Aguilar et al. 2008).

METHODS

Study Sites.—Nests of White-throated and
Clay-colored thrushes were located from 1999 to
2002 and monitored throughout Las Alturas, a
private forest reserve (08° 56' N, 82° 51' W) at
~1,300 m asl in southern Costa Rica. Systematic
nest searching was conducted in 1999 in two
abandoned coffee plots, each of 6 ha, in large
fields. We expanded the two coffee plots in 2000
to 10.3 and 13.3 ha. We also added two pasture
plots, one of 17.9 ha and one of 13.2 ha. We
searched the four plots from 2000 to 2002. Coffee
plots were in plantations that had been abandoned
in the mid-1990s and consisted of 1 to 3-m tall
coffee plants with a light overstory consisting
mainly of 5 to 7-m tall Erthyrina spp. The
understory in the plantations was variable al¬
though it tended to be sparse between the coffee
plants, i.e., there was little vegetation to impede
the movements of nest searchers. Pasture plots
were in plantations that had been abandoned
earlier in the season (e.g., Yahner and Scott 1988) and for
nests at lower heights. These expectations were
based partly on findings from other studies (e.g.,
Sörström et al. 1998) and partly from our
previous work indicating that toucans and raptors
are important predators in this system (Cohen and
Lindell 2004; C. A. Lindell, pers. obs.) and might
be more likely to detect high than low nests. We
also expected greater success for nests initiated
earlier in the season (e.g., Nur et al. 2004). Nest
height and concealment were measured for each
nesting attempt.

Nest Searching and Monitoring.—Nest search¬
ing started in late March-early April and continued
through August from 1999 to 2002, coinciding with
the nesting seasons of White-throated and Clay-
colored thrushes. Once found, nests were checked
every 2-4 days. Nests were not approached when
potential predators were present. We only re¬
mained near nests for sufficient time to ascertain
their contents. A nest was considered to have failed
when nestlings were missing before the age at
which they could have fledged. Successful nests
were those at which nestlings could have reached
the age of fledging and other evidence of fledging
was present including a flattened nest rim, feces on
the rim, or fledglings in the vicinity of the nest.
Nests were considered to have uncertain fate when
nestlings could have reached the age of fledging
but there was no other evidence of a successful
nesting attempt.

Nest Site Characteristics.—We investigated
characteristics that were likely to be important
in our system including nest concealment, nest
height, nest substrate (ground vs. vegetation), nest
initiation interval, and year. Our expectations
were that greater concealment (e.g., Martin 1993)
would positively influence the likelihood of nest
success. We also expected greater success for
nests on the ground compared to those in
vegetation (e.g., Yahner and Scott 1988) and for
nests at lower heights. These expectations were
based partly on findings from other studies (e.g.,
Sörström et al. 1998) and partly from our
previous work indicating that toucans and raptors
are important predators in this system (Cohen and
Lindell 2004; C. A. Lindell, pers. obs.) and might
be more likely to detect high than low nests. We
also expected greater success for nests initiated
earlier in the season (e.g., Nur et al. 2004). Nest
height and concealment were measured for each
nesting attempt.

Nest height (m) was measured from the ground
to the bottom of the nest. Nests built on the
ground or in a bank had a height of zero. Nests
were grouped into three height intervals: low =
0-1.5 m, medium = 1.6-2.4 m, and high = 2.5-
3.5 m. Nests >3.5 m could not be checked and
were not monitored. Concealment was catego¬
rized on a 1 to 4 scale (1 = <25% concealment, 2
= 26-50%, 3 = 51-75%, and 4 = 76-100%).
Concealment was estimated by an observer 1 m
from the north, south, east, and west sides of the
nest. Concealment estimates were also made from
1 m above and below nests when possible. Nests
on the ground were given a concealment estimate
of 4 from below. We calculated a mean of the six
readings for each nest to generate one value
between one and four for each nest. These values
were divided into three categories: low conceal¬
ment (0-1.99), medium concealment (2-2.99),
and high concealment (3-3.99).

Data Analysis.—White-throated and Clay-col¬
cored thrush nests were found in pasture, coffee,
forest fragments, and along roads at Las Alturas.
Sample sizes were small for both species in forest
fragments and for Clay-colored Thrush nests
along roads: nests from these land-cover types
were excluded from analyses.
TABLE 1. Influence of nest substrate, concealment, nest height, and year on White-throated Thrush nest survival, based on Cox proportional hazard regression model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter estimate ± SE</th>
<th>X²-value</th>
<th>P-value</th>
<th>Hazard ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest substrate</td>
<td>0.7513 ± 0.3037</td>
<td>6.1202</td>
<td>0.013</td>
<td>2.120</td>
</tr>
<tr>
<td>Concealment</td>
<td>-0.3185 ± 0.1024</td>
<td>9.6710</td>
<td>0.002</td>
<td>0.727</td>
</tr>
<tr>
<td>Nest height</td>
<td>0.5226 ± 0.1598</td>
<td>10.6957</td>
<td>0.001</td>
<td>1.686</td>
</tr>
<tr>
<td>Year</td>
<td>0.3700 ± 0.1426</td>
<td>6.7373</td>
<td>0.009</td>
<td>1.448</td>
</tr>
</tbody>
</table>

We randomly selected one of the nesting attempts for use in analyses when a nest was used more than once during a year. A few nesting attempts were excluded from analyses if uncertainty about the nest initiation date was too great: for example, if eggs were detected 1 day and not again and no parent was ever seen. The nestling period for both species is known to be 14 days (Cohen and Lindell 2004; C. A. Lindell, unpubl. data) and we calculated an average incubation period of 12 days for both species based on data from the present study. We calculated a range of possible laying and hatching dates for each nesting attempt based on contents from nest checks. Nest initiation dates were grouped into 7-day intervals for each year. The first interval started with the earliest nesting attempt. For example, the earliest laying date occurred on 17 March and the first interval was 15–21 March. The second interval was 22–28 March. Intervals were created until all nests were included.

We used Cox proportional hazard regression models to examine relationships between land-cover (coffee, pasture, road), year (1999–2002), nest height, concealment, nest substrate (ground or vegetation), nest initiation interval (when first egg was laid), and survival of nests. This type of regression model does not assume a particular distribution or constant mortality (Allison 2010) and nests that were observed for longer periods of time are weighted more heavily. We initially conducted univariate analyses to test the potential effects of land-cover, year, nest height, concealment, nest substrate, and nest initiation interval on nest survival. PROC PHREG was used for continuous variables while PROC LIFETEST was used for categorical variables (SAS Institute 2003, Allison 2010). Those variables with P-values <0.20 were included in further multivariable models. The multi-variable models tested included year, nest height, concealment, substrate, and each two-variable interaction for White-throated Thrushes and land-cover, nest height, and the interaction between these two variables for Clay-colored Thrushes. Our final models included only variables that were significant at P < 0.05. Variables in the final models met the assumption of proportionality (Allison 2010).

Sample sizes at the Rio Negro plantation were limited and from only 1 year. We did not test for the influence of particular variables on nest success but calculated daily mortality rates (DMRs) for nests of both species at this site using the Mayfield Method (Mayfield 1975, Johnson 1979), having calculated exposure days for attempts with successful, failed, and uncertain outcomes following Manolis et al. (2000). We also calculated DMRs for categories of nests from Las Alturas for those variables that were included in final Cox regression models. Nest success rates were calculated by subtracting DMRs from 1 to obtain the daily survival rate, and then raising this rate to the number of days in the incubation and nestling periods, i.e., 26 for both species (Mayfield 1975).

RESULTS

We found 351 White-throated Thrush nesting attempts at Las Alturas over the 4-year period in abandoned coffee (n = 179), pasture (n = 96), roads (n = 64), and forest fragments (n = 12). Ninety Clay-colored Thrush nesting attempts were observed in coffee (n = 66), pasture (n = 22), and roads (n = 2). Numbers of nesting attempts included in the analyses are lower because attempts missing data for a variable being tested were not included.

Nest Success.—The final model for White-throated Thrush included data from 317 White-throated Thrush nesting attempts and, for Clay-colored Thrushes, 88 attempts. Substrate, concealment, nest height, and year significantly influenced White-throated Thrush nest survival (Table 1). Hazard ratios indicate that: (1) nesting attempts in vegetation had a 112% greater rate of failure than those on the ground, (2) nesting
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TABLE 2. Daily mortality rates (exposure days) of White-throated Thrush nests at Las Alturas by substrate, concealment, height, and year and of Clay-colored Thrush nests by land-cover type. Only DMRs for those variables in final Cox regression models are included.

<table>
<thead>
<tr>
<th>Year</th>
<th>Daily mortality rate ± SE (White-throated Thrush)</th>
<th>Nest success rate (%)</th>
<th>Daily mortality rate ± SE (Clay-colored Thrush)</th>
<th>Nest success rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground</td>
<td>0.088 ± 0.005 (1.955)</td>
<td>21.2</td>
<td>0.096 ± 0.012 (560.5)</td>
<td>7.3</td>
</tr>
<tr>
<td>Vegetation</td>
<td>0.076 ± 0.007 (1.520)</td>
<td>12.8</td>
<td>0.054 ± 0.014 (275.5)</td>
<td>23.6</td>
</tr>
<tr>
<td>Concealment low</td>
<td>0.090 ± 0.017 (288)</td>
<td>8.6</td>
<td>0.037 ± 0.018 (109)</td>
<td>37.5</td>
</tr>
<tr>
<td>Concealment medium</td>
<td>0.077 ± 0.039 (941)</td>
<td>12.5</td>
<td>0.049 ± 0.008 (809.5)</td>
<td>27.1</td>
</tr>
<tr>
<td>Concealment high</td>
<td>0.058 ± 0.005 (2.246)</td>
<td>21.2</td>
<td>0.077 ± 0.008 (11,121.5)</td>
<td>12.5</td>
</tr>
<tr>
<td>Height low</td>
<td>0.059 ± 0.004 (2.889.5)</td>
<td>20.6</td>
<td>0.068 ± 0.007 (1,435)</td>
<td>16.0</td>
</tr>
<tr>
<td>Height medium</td>
<td>0.100 ± 0.013 (501)</td>
<td>6.5</td>
<td>0.118 ± 0.035 (84.5)</td>
<td>3.8</td>
</tr>
<tr>
<td>Height high</td>
<td>0.118 ± 0.005 (2.246)</td>
<td>12.5</td>
<td>0.100 ± 0.013 (501)</td>
<td>6.5</td>
</tr>
<tr>
<td>1999</td>
<td>0.097 ± 0.008 (109)</td>
<td>37.5</td>
<td>0.037 ± 0.018 (109)</td>
<td>37.5</td>
</tr>
<tr>
<td>2000</td>
<td>0.097 ± 0.008 (109)</td>
<td>37.5</td>
<td>0.037 ± 0.018 (109)</td>
<td>37.5</td>
</tr>
<tr>
<td>2001</td>
<td>0.097 ± 0.008 (109)</td>
<td>37.5</td>
<td>0.037 ± 0.018 (109)</td>
<td>37.5</td>
</tr>
<tr>
<td>2002</td>
<td>0.097 ± 0.008 (109)</td>
<td>37.5</td>
<td>0.037 ± 0.018 (109)</td>
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</tr>
<tr>
<td>Coffee</td>
<td>0.096 ± 0.012 (560.5)</td>
<td>7.3</td>
<td>0.054 ± 0.014 (275.5)</td>
<td>23.6</td>
</tr>
<tr>
<td>Pasture</td>
<td>0.088 ± 0.005 (1.955)</td>
<td>21.2</td>
<td>0.096 ± 0.012 (560.5)</td>
<td>7.3</td>
</tr>
</tbody>
</table>

The low height category includes both ground nests and those above the ground up to 1.5 m. When ground nests are excluded from calculations, the DMR for low nests is still lower than those for higher height categories (DMR = 0.061 ± 0.009, n = 934.5 exposure days).

The final Clay-colored Thrush model included only land-cover type, which was a marginally significant influence on nest survival (P = 0.0567, β = -0.4714, χ² = 3.6308; Table 2). The hazard ratio for the land-cover variable was 0.624, indicating nesting attempts in coffee had a 38.6% greater rate of failing than those in pasture; consequently, DMRs for nests in coffee were higher than in pasture (Table 2). The overall DMR for Clay-colored Thrush nests at Las Alturas was 0.084 ± 0.010 (n = 347 exposure days), or an expected nest success rate of 16.9%. DMRs for categories of White-throated Thrush nesting attempts varied (Table 2).

The final Clay-colored Thrush model included only land-cover type, which was a marginally significant influence on nest survival (P = 0.0567, β = -0.4714, χ² = 3.6308; Table 2). The hazard ratio for the land-cover variable was 0.624, indicating nesting attempts in coffee had a 38.6% greater rate of failing than those in pasture; consequently, DMRs for nests in coffee were higher than in pasture (Table 2). The overall DMR for Clay-colored Thrush nests at Las Alturas was 0.084 ± 0.010 (n = 347 exposure days), or an expected nest success rate of 16.9%.

Daily mortality rates at Rio Negro were approximately an order of magnitude lower than at Las Alturas: 0.006 ± 0.004 for White-throated Thrush (n = 18 nests and 318.5 exposure days) for an expected nest success rate of 98.5%, and 0.015 ± 0.015 for Clay-colored Thrush (n = 6 nesting attempts and 67 exposure days) for an expected nest success rate of 67.5%. All White-throated Thrush nesting attempts at Rio Negro were in vegetation rather than on the ground and all nests where concealment was measured were in the highest concealment category (n = 15). Sixty-seven percent of the attempts were in the lowest height category and the other 33% were in the medium height category (n = 15; 3 nests were not measured because attempts were still occurring when the field season ended). Clay-colored Thrush nesting attempts were all in vegetation, five of six were in the highest concealment category, and five of six were in the medium height category.

DISCUSSION

Our first objective was to compare nest success of Clay-colored and White-throated thrushes in two land-cover types, coffee and pasture, that cover large areas of the Neotropics. Clear differences in nest success would facilitate ranking the relative value of these land-covers as nesting habitat for these species. Our results indicated that nest success was site-specific and varied with nest-site characteristics, making conservation recommendations based on land-cover type elusive, and underscoring the necessity of investigating environmental influences on nest success at multiple scales.

We expected daily mortality rates (DMRs) would be greater for nests in coffee than pasture (Lindell and Smith 2003). The results for Clay-
colored Thrush support this prediction although those for White-throated Thrush indicate that local-scale nest site characteristics were greater influences on nest success than land-cover type. White-throated Thrush ground nests were safer than those in vegetation in either land-cover type. Ground nests at Las Alturas were typically built into steep banks, which we assume protected them from being stepped on by livestock. DMR increased with increasing nest height, even when ground nests were excluded from analyses, i.e., nests low in the vegetation were safer than nests higher in the vegetation.

Higher DMRs for White-throated Thrush nesting attempts that were above the ground, higher in the vegetation, and with low levels of concealment suggest that predatory birds may be an important influence on nest success. Hawks and toucans were frequently observed perching in the overstory of the coffee, apparently scanning for movement, and a toucan was observed eating nestlings (Cohen and Lindell 2004; C. A. Lindell, pers. obs.). Snakes were likely important nest predators as well (Cohen and Lindell 2004). Our results indicate our measurements of concealment were positively correlated with the way some nest predators perceived nests.

Nest initiation date was not in the final model for either species, similar to a previous study that found no seasonal variation in nest predation (Young 1994). This suggests a possible difference in seasonal effects on nest success between tropical and temperate-nesting populations (Nur et al. 2004).

Overall White-throated and Clay-colored thrush nest success rates at Las Alturas (16.9 and 10.2%, respectively) are comparable to some of the lower rates that have been reported for neotropical species. The nest success rate for 43 species combined in tropical lowland forest in Costa Rica was 24.4% (Young et al. 2008) and ranged from 8.3 to 71.6% for 10 species in lowland forest in Panama (Robinson et al. 2000). In contrast, success rates for both thrush species in the active coffee plantation at Rio Negro were high (98.5 and 67.5% for White-throated and Clay-colored thrushes, respectively). Only three of 24 thrush nesting attempts at Rio Negro were documented as failures. We suggest these results indicate two points deserving further investigation. First, all but one of the Rio Negro nests were in the highest concealment category. The coffee plants at this site were under active cultivation and tended to be more leafy and compact than those at Las Alturas, providing more concealment for nests. This pattern, along with the inclusion of concealment in the White-throated Thrush nest success model, suggests concealment may be a particularly important influence on tropical nest success. Second, the area around Rio Negro is much less forested and has a greater human population density than Las Alturas. These two factors potentially result in reduced habitat for predatory birds and snakes, and greater hunting pressure on these species, diminishing predation pressure on nesting birds.

CONSERVATION IMPLICATIONS

Conservation recommendations based on land-cover type would be relatively easy if we could rank land-covers as to the quality of habitat they provide for target species and if rankings were consistent across species. Our results indicate these conditions are not met for these species. Clay-colored Thrush nest success was lower in abandoned coffee than pasture at our primary study site, but nest success was high at an active coffee plantation; a simple dichotomy of coffee and pasture could not predict nest success. White-throated Thrush nest success varied substantially with local-scale nest-site characteristics. Thus, for this species, variation within a land-cover type influenced nest success more than variation among land-cover types. In addition, hunting pressure for predatory birds and snakes, and landscape features such as forest cover potentially influenced nest success.

White-throated Thrush nests that were well-concealed, either because of vegetation near the nest or because of an inconspicuous location within a bank, had higher probabilities of success than less-concealed nests. Maintaining features that help conceal nests, in the form of dense foliage and the existence of vines and moss (Stiles and Skutch 1989), and or the existence of steep banks, should contribute to White-throated Thrush nest success more than land-cover type.

We suggest focusing resources in three ways to make progress in understanding the factors that influence nesting success of tropical birds and in providing conservation recommendations to tropical property owners and land managers.

1. Focus on species of conservation significance with nests that can be found and monitored in reasonable numbers.
2. Assess the extent to which focal species' nest success, as a function of environmental characteristics, corresponds to that of other species.

3. Investigate how characteristics of the environment at multiple scales influence nest success (Tozer et al. 2010).

Specifically, future work should compare nest success across a range of land-cover types, in several landscapes, and characterize nest success as a function of local- and landscape-scale features.

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LITERATURE CITED


NOCTURNAL PROVISIONING BY SWAINSON’S THRUSH

JEFFREY R. BALL, KATRINA C. LUKIANCHUK, AND ERIN M. BAYNE

ABSTRACT.—We studied Swainson’s Thrush (Catharus ustulatus) at two study areas of different latitudes to examine if parents provisioned their nestlings beyond daylight hours. We viewed 591 hrs of video from 37 nests. All nests were provisioned outside the dawn to dusk period but provisioning also continued through the night at the northern site. Night provisioners made an average (± SE) of 1.55 ± 0.18 fewer provisioning trips/hr during the pre-dawn to late evening periods compared to non-night provisioners. Night provisioners compensated with two additional trips/hr during the post-dusk period and 2.11 (95% CI: 1.61–2.77) trips/hr during the night period. Night provisioners did not experience improved reproductive success, which supports our conclusion that night provisioning was compensatory rather than ‘bonus’ energy. Night provisioning was best explained by increased day length, which corresponded to increased light levels during the night period that enabled parents to navigate and locate food. Swainson’s Thrush extend a given provisioning effort over more hours as light levels permit rather than increasing energy delivery to their nestlings, which may provide time and energy for other activities. Received 27 August 2010. Accepted 18 January 2011.

Foraging and acquisition of energy are important to animal survival. However, energy acquisition often conflicts with other activities that are important components of fitness including avoiding predators (Lima and Dill 1990), provisioning dependent young (Ydenberg 1994), and maintaining social bonds (Dunbar et al. 2009). Individuals are expected to tradeoff foraging with other fitness related activities subject to ensuring their energy needs are met (Houston and McNamara 1985, 1999; Dunbar et al. 2009). The decision to spend time on alternate activities depends, in part, on the individual’s current energy state and time available to acquire sufficient resources to survive an extended period of forced fasting (Stephens 1981).

The active period of songbirds is assumed to be largely restricted to daytime hours (i.e., between dawn and dusk) when the available light affords the visual acuity necessary to perform complex tasks such as navigating and locating food. Individuals able to extend the length of their active period would have an advantage in balancing energy acquisition with other activities. The intensity and duration of light available outside of daytime hours varies considerably over space and time depending on moon phase, cloud and canopy cover, and date and latitude (Martin 1990). Visual acuity increases with light availability and individuals in open habitats at high latitudes during the summer solstice with a full moon under clear sky conditions have the greatest potential to extend the length of their active period.

Additional active time allows parents with dependent young more opportunity to meet their energy needs and the energy needs of their brood (Ydenberg 1994). Parents may use additional foraging time to compensate for an energy shortfall due to poor food quality, low food abundance, inclement weather (McCarty and Winkler 1999), and/or to avoid predation risk (Eggers et al. 2005) during day-time hours. Extending the active period could also allow parents time to provide additional ‘bonus’ energy to their nestlings, which could lead to larger broods (Drent and Daan 1980), increased growth rates, a shortened pre-fledging period (Searcy et al. 2004), and improved probability of surviving post-fledging period (Monros et al. 2002).

We studied nestling provisioning rates by parent Swainson’s Thrush (Catharus ustulatus) at two study areas of different latitude to examine: (1) if hourly provisioning rates during the day and night varied between study areas; (2) if nocturnal provisioners fed their nestlings at lower rates during the day; (3) what factors were associated with variation in nocturnal provisioning rate; and (4) if nocturnal provisioning improved reproductive success.

METHODS

Study Area.—We established 15 plots in mature mixedwood forest in two study sites in the boreal forest of western Canada. Six 42-ha plots were near Fort Simpson, Northwest Territories (61° 52' N, 121° 20' W) in 2005 and 2006, and nine 24-ha plots were in the Chinchaga forestry region.
northwest of Manning, Alberta (57°18’N, 118°23’W) in 2006 and 2007. The Fort Simpson study site was >500 km north of Chinchaga and had ~19.7 hrs of daylight at the summer solstice compared to 18 hrs of daylight at Chinchaga.

Field Procedures.—We visited each study plot every 3 days between late May and mid-July to search for and to monitor nests. We randomly selected 37 Swainson’s Thrush nests for video monitoring and placed an infrared digital video camera at each nest to continuously and unobtrusively record parental behaviors. We observed each brood at ~4 and 8 days of age to account for age-related changes in nestling energy demand (Weathers 1996). Age estimates for each brood were based on video footage and hatch date estimates from repeat nest visits. We viewed nine 1-hr time periods during each age. Six diurnal periods had start times evenly distributed between 1 hr post-sunset and 2 hrs pre-sunset. Three nocturnal periods had start times at sunset, 2 hrs post-sunset, which was approximately the middle of the night, and 1 hr prior to sunrise (hereafter post-dusk, night, and pre-dawn, respectively). We quantified provisioning rate (number of food deliveries to the nest/hr), nestling age as a continuous variable, and the average number of nestlings present for each time period. We were unable to consistently identify the size of prey items and no attempt was made to estimate rates of biomass or energy delivery. Nest fate and nestling age were not transformed.

We compared support among six models to models that included a binary variable identifying pairs as night provisioners or non-night provisioners, which we added either as a main effect or as an interaction with time period. These analyses were performed on a subset of data that excluded the first fledgling from video footage, A nest was considered successful if ~1 nestling fledged, which we defined as departing the nest under its own power. Age of fledgling refers to age at which the first fledgling left the nest.

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We quantified three covariates that we expected might influence nocturnal provisioning. Canopy tree density/m² reflects habitat complexity and potential light availability to the forest understory. We counted the number of trees ≥3 m in height within an 11.3-m radius around each nest (Martin et al. 1997). We expected large openings in the forest canopy to similarly influence nocturnal visibility and navigability. We used ArcGIS (ESRI 2009) to calculate the distance between each nest and the nearest canopy edge created by a pipeline, seismic line, road, or river. Finally, we expected nestling energy demand and the need for provisioning to increase during colder temperatures. We placed a weather station (ONSET 2006) at the center of each study area under a forest canopy similar to the study plots and measured temperature at 5-min intervals. Temperature data were averaged/hr for each time period that provisioning was observed.

Statistical Analyses.—All covariates were tested for normality using normal probability plots and a combined test of skewness and kurtosis (D’Agostino et al. 1990, Royston 1991, Zuur et al. 2009). Nestling number was squared to achieve normality (χ² = 0.23, P = 0.89). We applied square root and log transformations to edge distance and tree density, respectively, to improve skewness and kurtosis. Temperature, day length, and nestling age were not transformed.

We compared support for our base model to models that considered the effect of time period, study area, and an interaction between time period and study area.
Table 1. Candidate model set accounting for variation in hourly provisioning rate among nine time periods at two study sites, Fort Simpson, NT and Chinchaga, AB. Data include 591 hrs of observations from 37 Swainson’s Thrush nests.

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ΔICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base + study site × time period</td>
<td>-1,279.83</td>
<td>24</td>
<td>2,603.29</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Base + time period</td>
<td>-1,314.07</td>
<td>12</td>
<td>2,652.68</td>
<td>49.38</td>
<td>1.89 × 10^-3</td>
</tr>
<tr>
<td>Base</td>
<td>-1,568.99</td>
<td>4</td>
<td>3,146.05</td>
<td>542.76</td>
<td>1.38 × 10^-8</td>
</tr>
<tr>
<td>Base + study site</td>
<td>-1,568.91</td>
<td>5</td>
<td>3,147.92</td>
<td>545.62</td>
<td>5.45 × 10^-10</td>
</tr>
</tbody>
</table>

* Base model includes nestling age + nestling number.
* Model likelihood given data x = exp(-0.5 ΔAICc).

The evidence ratio in support of this interaction model was 5.29 × 10^-10 over the next best supported model. The overwhelming support for this model occurred because provisioning during the night period was not recorded at Chinchaga. Removing the night period from the analysis did not provide support for a study area by time period interaction (Fig. 1) indicating similar prey delivery rates at all other times in the two study areas.

We found weak evidence that nests provisioned during the night period had lower provisioning rates during six of seven remaining periods compared to nests not provisioned during the night period (Table 2). We restricted these analyses to Fort Simpson where we recorded provisioning during the night period and excluded the single observation day with camera failure. The best supported model included night provisioner (i.e., provisioned during the night period) status as an interaction with time period. The AICc values of all models in the candidate set were within 2.25 suggesting addition of night provisioner status added little explanatory power to the overall model. The evidence ratio indicates the interaction model was 3.1 times more likely compared to the base model. Support for the interaction reflects an increased provisioning rate of ~2/hr by night provisioners over non-night provisioners during post-dusk compared to other periods (Fig. 2). Non-night provisioners made an average (± SE) of 1.55 ± 0.18 additional provisioning trips/hr compared to night provisioners during the remaining periods (pre-dawn to late pm). Night provisioners made an estimated 2.11 (95% CI: 1.61–2.77) trips/hr during the night period.

**RESULTS**

We viewed 591 hrs of video from 37 nests. Twenty-nine nests were viewed at ~4 and 8 days of age whereas eight nests were only available to be viewed at one age. We viewed all nine time periods for 34 nests. We were unable to view the night period on three occasions, once at Fort Simpson and twice at Chinchaga, because of camera infrared failure. We excluded these days from all analyses focused on night provisioning.

Variation in hourly provisioning rate was best explained by addition of an interaction between study area and time period to the base model (Table 1). The evidence ratio in support of this interaction model was 5.29 × 10^-10 over the next best supported model. The overwhelming support for this model occurred because provisioning during the night period was not recorded at Chinchaga. Removing the night period from the analysis did not provide support for a study area by time period interaction (Fig. 1) indicating similar prey delivery rates at all other times in the two study areas.

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**Figure 1.** Predicted hourly provisioning rate by Swainson’s Thrush at Fort Simpson, NT (gray bars), and Chinchaga, AB (white bars) from the best-fitting model (Table 1). Nestling age and nestling number are set to average values of 6.19 and 3.60, respectively.
TABLE 2. Candidate model set assessing whether pre-dawn to post-dusk hourly provisioning rates varied based on night provisioning status (yes or no) to examine if night provisioners were compensating for an energy delivery shortfall during the day or providing additional “bonus” energy to their nestlings. Data are restricted to Fort Simpson, NT and include 24 hr of observations from 20 nests.

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>K</th>
<th>ΔAICc</th>
<th>ΔΔAICc</th>
<th>LRmodelP</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base + night provisioner × time period</td>
<td>-680.17</td>
<td>19</td>
<td>1.401.10</td>
<td>0.00</td>
<td>1.00</td>
<td>0.46</td>
</tr>
<tr>
<td>Base + night provisioner</td>
<td>-688.17</td>
<td>12</td>
<td>1.401.44</td>
<td>0.34</td>
<td>0.84</td>
<td>0.39</td>
</tr>
<tr>
<td>Base</td>
<td>-690.21</td>
<td>11</td>
<td>1.403.35</td>
<td>2.25</td>
<td>0.32</td>
<td>0.15</td>
</tr>
</tbody>
</table>

1 Rate model includes nestling age * nestling number * time period.
2 Model likelihood given data x = exp(-AAICc).

A model that considered day length alone received overwhelming support for explaining variation in provisioning rate during the night period at Fort Simpson (Table 3). Provisioning rate increased sharply from zero when day length exceeded 19.3 hrs (Fig. 3). Only the full model received more support (ΔAICc = 0.97) but the small evidence ratio (1.62) suggests little improvement over the more parsimonious day length model. Temperature also explained some variation in provisioning rate during the night period. The evidence ratio of the temperature-only model was 59 times that of the base brood demand model and the linear temperature coefficient did not include zero in its confidence interval (95% CI: ~0.23–0.02). Increasing temperature from 8 to 18°C, which was the approximate range of night temperature at Fort Simpson, reduced the predicted night provisioning rate from 3.03 (95% CI: 1.50–6.12) to 0.85/hr (95% CI: 0.42–1.73).

Twenty-nine nests successfully fledged one or more young. We did not record provisioning during the night period at Chinchaga and were unable to include study area as a covariate in our reproductive success models. We assessed the effects of night provisioner status on reproductive performance for all nests combined and for Fort Simpson nests only. Results for Fort Simpson were similar to those for all nests. We found no evidence that nests provisioned during the night period had improved reproductive success. Night provisioning did not affect the probability of being successful ($\chi^2_1 = 0.38$, $P = 0.54$), the number of young fledged from successful nests ($\chi^2_1 = 0.06$, $P = 0.81$), or age at fledging ($F_{27} = 0.66$, $P = 0.42$; Fig. 4).

**DISCUSSION**

Our data clearly demonstrate the provisioning period for Swainson’s Thrush is not restricted to the hours between dawn and dusk. Pairs extend provisioning well before sunrise and well after sunset, particularly at higher latitudes where provisioning continues through the night. Intuitively this result is not surprising given the tendency of many songbird species, including Swainson’s Thrush, to migrate at night (Mack and Wang 2000, Newton 2008). Some nocturnal migrants possess a special brain function that enhances night vision outside of the migratory period (Mouritsen et al. 2005), which would enable parents to extend their provisioning period. However, migratory flights are in open skies and likely require less visual acuity than navigating and foraging in a forest. This may explain why we did not record night provisioning until day length exceeded 19.3 hrs. This threshold approximates the day length at the latitude of our northern site.
TABLE 3. Candidate model set accounting for variation in provisioning rate during the night period by Swainson’s Thrush at Fort Simpson, NT (20 nests, 37 time periods).

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>K</th>
<th>ΔAIC</th>
<th>ΔAIC_c</th>
<th>L(model)_c</th>
<th>ΔAIC_c</th>
</tr>
</thead>
<tbody>
<tr>
<td>All parameters</td>
<td>-45.06</td>
<td>8</td>
<td>111.27</td>
<td>0.00</td>
<td>1.00</td>
<td>0.62</td>
</tr>
<tr>
<td>Day length</td>
<td>-52.75</td>
<td>3</td>
<td>112.23</td>
<td>0.97</td>
<td>0.62</td>
<td>0.38</td>
</tr>
<tr>
<td>Temperature</td>
<td>-59.20</td>
<td>3</td>
<td>125.13</td>
<td>13.86</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Edge distance</td>
<td>-60.95</td>
<td>3</td>
<td>128.63</td>
<td>17.36</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Canopy tree density</td>
<td>-61.90</td>
<td>3</td>
<td>130.53</td>
<td>19.26</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Nestling age + nestling number</td>
<td>-62.02</td>
<td>4</td>
<td>133.28</td>
<td>22.01</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

* Model likelihood given data: $\hat{\ell} = \exp(-\frac{1}{2} \Delta AIC_c)$.

(19.08 hrs) when civil twilight extends through the night (i.e., nautical twilight does not occur) suggesting some ambient light is required for nocturnal foraging. A similar threshold does not exist at Chinchaga where 3.67 hrs were darker than civil twilight at the solstice. No birds were recorded feeding during the night period at Chinchaga because all observations were darker than civil twilight. We did not find support for forest structure covariates (edge proximity and canopy density) affecting ambient light availability and nocturnal provisioning rate; non-forest songbirds may require even less light and may be able to extend their provisioning period further in open habitats.

Night provisioners are compensating for a lower rate of energy delivery during the day compared to non-night provisioners rather than delivering additional ‘bonus’ energy. This agrees with our finding that night-provisioned nests are not more successful or more productive than nests not provisioned during the night period. It is unlikely that night provisioners are having greater difficulty meeting their brood’s energy needs during the day given that days are longer. A more plausible explanation for compensation is that night provisioning parents are distributing an equal and sufficient amount of chick-rearing effort over more active hours, resulting in a lower hourly rate of provisioning but similar total provisioning over the entire day. It is not clear why parents do not take

![Figure 3](image3.png)

**FIG. 3.** Provisioning rate by Swainson’s Thrush during the night-time period with increasing day length at Fort Simpson, NT. The observed provisioning rate (points) was quantified from 37 hours of observation at 20 nests. The estimated provisioning rate (line) is from a mixed-effects Poisson regression model that only considered the effect of day length with nest identity as a random effect.

![Figure 4](image4.png)

**FIG. 4.** Average number of fledglings and average age at fledging from 29 successful Swainson’s Thrush nests based on study area and night provisioning status.
advantage of a longer active period by delivering more energy. Perhaps chick growth or digestive capacity was maximized and additional resources would be wasted. Alternatively, parents may have been provisioning at some optimal working capacity given the time and food resources available to fuel their own effort (Drent and Daan 1980, Ydenberg 1994). We found little evidence of chick starvation in either study area (IRB, unpubl. data) suggesting that parents were not having difficulty meeting their chick’s energy needs. An extended provisioning period may improve reproductive performance if this was not the case.

We did not find improvements in reproductive performance but we cannot conclude that other fitness benefits were not realized by parents that provisioned during the night period. Night-fed nestlings may have been heavier or structurally larger than non-night fed nestlings, which could increase their probability of surviving fledging (Monros et al. 2002). A longer active period and lower hourly provisioning rate could allow night-provisioning parents more time to forage for themselves, which could increase survival through improvements in body condition and reduced risk-taking behavior. A lower hourly provisioning rate also would allow time for alternate fitness-related activities such as territorial defense, predator vigilance, or social interactions. We suggest researchers recognize the potential that birds can extend their active period well beyond the dawn to dusk period when comparing hourly provisioning rates between regions at different latitudes. We also suggest researchers consider fitness-related opportunities other than nesting success that may be provided by a lower hourly provision rate.

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LITERATURE CITED


ONSET. 2006, HOBO Weather Station Data Logger 1121-001, ONSET Computer Corporation, Bourne, Massachusetts, USA.


PROVISIONING BEHAVIOR OF MALE AND FEMALE GRASSHOPPER SPARROWS

JENNIFER ADLER$^1$ AND GARY RITCHISON$^{1,2}$

ABSTRACT.—We examined the provisioning behavior of male and female Grasshopper Sparrows (Ammodramus savannarum) during 2002 and 2003 by videotaping nests ($n = 15$) and subsequently reviewing tapes to quantify provisioning rates and identify prey items. There was no difference in provisioning rates of male and female Grasshopper Sparrows ($P = 0.13$) with mean rates of 2.16 visits/hr for females and 1.86 visits/hr for males. Provisioning rates for males and females combined varied with nestling age ($P = 0.01$) with rates lower for 1-4-day-old nestlings, increasing through day 6 and then declining for 7-10-day-old nestlings. Provisioning rates varied with brood size ($P = 0.026$) with rates higher for broods of five than broods of three or four. Most prey items delivered to nestlings were grasshoppers (Orthoptera, 68.1%).

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The relative contribution of males and females in provisioning nestlings varies among species of songbirds. One parent may provision nestlings at higher rates than the other parent in some species (Grundel 1987, Cockburn 2006); whereas males and females contribute equally in other species (Rykken et al. 1996, Schadd and Ritchison 1998, Nordlund and Barber 2005). Variation among species suggests factors influencing parental investment may produce different provisioning strategies in different species.

Olson et al. (2008), in a comparative study involving data from 193 species of birds, reported parental care by males and females was negatively correlated; variance in male care was significantly higher than for female care. Thus, across species, variation in total care is primarily explained by differences in that provided by males. Several factors can influence male parental care. For example, males may reduce levels of parental care to pursue extrapair matings (Mitchell et al. 2007). Males in multi-brooded species may improve their reproductive success by provisioning nestlings in first broods, increasing the likelihood of their mates subsequently re-nesting (Stodola et al. 2009). Risk of nest predation may also influence male care as Bjornstad and Lifjeld (1996) suggested provisioning by male Willow Warblers (Phylloscopus trochilus) insured rapid growth of nestlings, early fledging, and reduced risk of nest predation. These and other factors can potentially influence male provisioning behavior, but their relative importance in explaining variation in male care among different species of birds remains unknown. Thus, studies are needed of species that vary in behavior (e.g., mating strategies and number of broods per breeding season) and nesting ecology (e.g., nest predation rates).

Previous studies indicate several factors, including variation in brood size and nestling age, can affect provisioning behavior of both males and females. Parents, for example, may increase provisioning rates as brood sizes increase (e.g., Bédard and Meunier 1983, Conrad and Robertson 1993) or there may be an inverse relationship between provisioning rate and brood size (e.g., East 1981, Trémont and Ford 2000). Some parents provision nestlings at similar rates throughout the nestling period (East 1981, Bédard and Meunier 1983, Schadd and Ritchison 1998), while others either continue to increase provisioning rates as nestlings grow (Nordlund and Barber 2005) or increase provisioning rates through the mid-nestling period before reducing rates a few days before fledging (East 1981, Conrad and Robertson 1993).

Grasshopper Sparrows (Ammodramus savannarum) are socially and genetically monogamous (Ammer 2003), and typically breed in grasslands and lightly grazed pastures (Vickery 1996). These sparrows nest on the ground with clutch and brood sizes ranging from three to five and typically have low nesting success (25-50%) (Vickery 1996). Grasshopper Sparrows are also multi-brooded (2-3 nests/breeding season) (Vickery 1996). Both males and females provision nestlings (Vickery 1996), but the relative contributions of each are unknown. The objectives of our study were to examine the possible effects of brood size, brood number, and nestling age on the provisioning behavior of male and female Grasshopper Sparrows.

METHODS

Study Area.—Our study was conducted from 1 May to 8 August 2002 and 30 April to 29 August...
2003 at the Blue Grass Army Depot (BGAD), 11 km southeast of Richmond, Madison County, Kentucky. The BGAD is a matrix of woodlots, open fields, and pastures.

Field Methods.—We captured Grasshopper Sparrows in mist nets beginning in early May, either using playback of conspecific songs to lure males into nets or flushing females into nets placed near nests. All captured sparrows were banded with a numbered USGS aluminum band plus a unique combination of three colored leg bands.

Nests were located by watching the behavior of adults, particularly adults carrying nesting material or food in their bills. Nests found during incubation were checked at least every 3 days until eggs hatched. A dummy camcorder was placed near the nest (1–1.5 m away) for at least 24 hrs just prior to or shortly after eggs hatched to acclimate adults to its presence.

Nests were videotaped using camcorders mounted on tripods. All taping was conducted during the morning and early afternoon (0700–1200 hrs). The mean ± SE duration of taping sessions (n = 108) was 3.1 ± 0.1 hrs. Four pairs of Grasshopper Sparrows re-nested and we videotaped both their first and second nests.

We viewed all videos and, for each adult visit to a nest, noted its gender (based on leg bands) and recorded the size, identity, and number of prey items delivered. Prey size was estimated by comparing the length of prey to the length of the adult’s beak. We estimated the length of prey delivered and multiplied prey length relative to the length of the bill by 11.4 mm (intermediate between the mean bill lengths of male 11.9 mm and female 10.9 mm) Grasshopper Sparrows (Crossman 1989). Prey items were identified to taxonomic order, except larval insects were classified as larvae. We estimated the amount of prey biomass delivered to nestlings using the formula: prey biomass = number of adult visits/hr x mean prey size x mean number of prey.

Statistical Analysis.—Repeated measures analysis of variance (ANOVA) was used in examine the effects of nesting age, brood size, and brood number on provisioning behavior (rates and prey biomass) of male and female Grasshopper Sparrows. We used Student-Newman-Keuls (SNK) multiple comparison tests to ascertain which means differed. Repeated measures ANOVA was also used to examine possible differences between males and females in provisioning behavior. Videotaping effort varied among nesting ages (i.e., sample sizes for some days were relatively small) and nestlings in some age groups were grouped into age categories (e.g., 1–2 days post-hatching) for some analyses. All analyses were performed using SAS statistical software (SAS Institute 1999). Values are presented as means ± SE.

RESULTS

We videotaped nests of 15 pairs of Grasshopper Sparrows during 2002 and 2003, including one nest each for 11 pairs and two nests for four pairs. Both nests were taped for the latter four pairs during the same breeding season (representing first and second broods). The mean number of nestlings per nest was 4.0 ± 0.2 (range = 3–5) with means of 4.2 ± 0.2 for first nests (n = 15) and 3.3 ± 0.3 for second nests (n = 4).

Female Grasshopper Sparrows made 629 visits to nests (41.5% of 1,516 total visits), whereas males made 531 visits (35.0% of visits). Vegetation obscured our view of some visiting adults and we were unable to identify visiting adults during 356 visits (23.5% of visits). There was no difference in provisioning rates between males and females (F1,13 = 2.6, P = 0.13) with mean provisioning rates of 2.16 ± 0.16 visits/hr for females (n = 93 observation periods) and 1.86 ± 0.14 visits/hr for males (n = 93 observation periods). There were no significant interactions between gender and brood number (first vs. second nest; P = 0.79) and gender and brood size (P = 0.22). The interaction between gender and nestling age approached significance (P = 0.053), but comparison of male and female provisioning rates did not reveal a clear trend (Fig. 1).
Grasshopper Sparrows varied with number of rates (SNK tests, \( P < 0.05 \)) for broods of five (6.7 ± 4.7, \( F = 0.6, P = 0.62 \)). Prey biomass delivered by adults varied with number of nestlings (\( F_{2,15} = 5.5, P = 0.016 \)); the amount of prey biomass delivered was significantly different (SNK tests, \( P < 0.05 \)) for broods of three (7.2 ± 0.7/hr), four (10.8 ± 1.0/hr), and five (14.1 ± 1.0/hr). We also found no difference among broods of different sizes in amount of prey biomass delivered by adults per nestling (\( F_{2,2} = 0.1, P = 0.90 \)).

**Brood Number.**—We found no difference in provisioning rates between broods (\( F_{1,3} = 1.0, P = 0.39 \)) for pairs of Grasshopper Sparrows (\( n = 4 \)) where both first and second nests were videotaped. We also found no interaction between nest number (first and second nests) and nestling age (\( P = 0.49 \)), indicating that adults provisioned nestlings of different ages at similar rates for both nests.

**Prey Items.**—We either could not ascertain if adult Grasshopper Sparrows delivered prey or could not identify the prey item during 771 of 1,744 nest visits (44.2%). Adults visited nests without prey 84 times (8.6% of visits) and delivered 960 identifiable prey items during 889 visits. One prey item was usually delivered per visit (\( n = 820 \) visits, or 92.3%) with two items delivered during 67 visits (7.5%) and three during two visits (0.2%).

Most prey (\( n = 960 \)) were grasshoppers (Orthoptera, Acrididae; \( n = 654, 68.1\% \)), larvae (\( n = 217, 22.6\% \)), crickets (Orthoptera, Gryllidae; \( n = 54, 5.6\% \)), and moths (Lepidoptera, \( n = 18, 1.9\% \)). Other prey items included seven bees (Hymenoptera, Apoidea), six beetles (Coleoptera), and four spiders (Araneae). Mean length of grasshoppers fed to nestlings was 24.4 mm and the mean length of crickets was 21.8 mm.

**DISCUSSION**

Male and female Grasshopper Sparrows provisioned nestlings at similar rates and delivered similar amounts of prey biomass. Similar results have been reported for other songbirds (e.g., Schad and Ritchison 1998, Nordlund and Barber 2005). However, in other species where both parents provision young (e.g., Bédard and Meunier 1983, Bouwman et al. 2005, Falconer et al. 2008), females provisioned at higher rates than males. Grasshopper Sparrows, at least among populations in southern West Virginia (Ammer 2003), appear to be both socially and genetically

<table>
<thead>
<tr>
<th>Nestling age (days)</th>
<th>Provisioning rate (visits/hr)*</th>
<th>Prey biomass/hr</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2</td>
<td>2.7 ± 0.5 (a)</td>
<td>5.5 ± 1.1 (a)</td>
</tr>
<tr>
<td>3</td>
<td>3.8 ± 0.5 (ab)</td>
<td>6.9 ± 1.3 (ab)</td>
</tr>
<tr>
<td>4</td>
<td>4.9 ± 0.4 (abc)</td>
<td>10.0 ± 1.0 (ab)</td>
</tr>
<tr>
<td>5</td>
<td>6.0 ± 0.8 (bc)</td>
<td>12.7 ± 1.9 (b1)</td>
</tr>
<tr>
<td>6</td>
<td>6.8 ± 0.7 (c)</td>
<td>13.8 ± 1.2 (b)</td>
</tr>
<tr>
<td>7</td>
<td>5.5 ± 0.6 (bc)</td>
<td>11.1 ± 1.5 (ab)</td>
</tr>
<tr>
<td>8-10</td>
<td>5.0 ± 0.6 (abc)</td>
<td>11.0 ± 1.8 (ab)</td>
</tr>
</tbody>
</table>

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* Mean ± SE means with the same letter are not significantly different; SNK test, \( P < 0.05 \).
monogamous and males likely can be certain of their paternity and may not seek extrapair copulations. Thus, providing parental care may be a better strategy for males to maximize reproductive success than seeking additional mating opportunities.

Several factors may influence provisioning behavior of male Grasshopper Sparrows. For example, nest predation rates for this species are typically high (50–75%) (Vickery 1996) and, as suggested for Willow Warblers (Bjornstad and Lifjeld 1996), provisioning by males may help insure rapid growth of nestlings, earlier fledging, and reduced risk of nest predation. In addition, Grasshopper Sparrows are typically multi-brooded and, as suggested for Black-throated Blue Warblers (Dendroica caerulescens) (Stodola et al. 2009), males may improve their reproductive success by provisioning nestlings in first broods to increase the likelihood of mates subsequently re-nesting.

Provisioning rates and amount of biomass delivered to nestlings by Grasshopper Sparrows in our study increased until day 6 and decreased prior to fledging (days 7–10 post-hatching). Similar variation in provisioning behavior has been reported in other songbirds, including European Robins (Erithacus rubecula) (East 1981) and Savannah Sparrows (Passerculus sandwichensis) (Bédard and Meunier 1983). Adult provisioning rates of other songbirds continue to increase with nestling age and are highest just before fledging (e.g., Grundel 1987, Goodhred and Holmes 1996, Yezerinac et al. 1996, Fillatier and Breitwisch 1997). Goodhred and Holmes (1996) suggested a positive relationship between nestling age and provisioning rate was due to increasing energy demands of the young, either for growth or thermoregulation.

The decline in provisioning rates of adult Grasshopper Sparrows near the end of the nestling period may be influenced by the risk of nest predation with adults encouraging or inducing fledging by reducing provisioning rates. Nestling Grasshopper Sparrows may leave nests to obtain food from adults approaching the nest (Young 1987), suggesting that inducing older nestlings to fledge may not be difficult. Young Grasshopper Sparrows are generally unable to fly when they first leave nests but are able to run (Smith 1963); mobile young able to run and hide in vegetation may be less susceptible to predation. The chances of an entire brood being lost to predation would likely be reduced once young have fledged.

Provisioning rates and amount of biomass delivered by adult Grasshopper Sparrows increased with increasing brood size. Thus, individual nestlings in broods of different size were provisioned at similar rates and received similar amounts of prey biomass. Kaspari (1991) studied a population of Grasshopper Sparrows in Nebraska and reported similar results. Provisioning of individual nestlings at similar rates, regardless of brood size, may enhance the reproductive success of adult Grasshopper Sparrows because mass at fledging is an important predictor of survival for young (Magrath 1991, Ringsby et al. 1998, Schwagmeyer and Mock 2008).

Our sample size for second nests was small (n = 4) and we found no effect of nest number (first vs. second) on the provisioning behavior of Grasshopper Sparrows. Similar results have been reported for other species of songbirds (e.g., MacColl and Hatchwell 2003, Nordlund and Barber 2005). Other investigators have reported lower provisioning rates for later broods (Royama 1966, Barba et al. 2009), although Stodola et al. (2009) reported provisioning rates for second broods may be higher than for first broods.

Grasshoppers were the most common prey delivered to nestlings with Lepidopteran larvae being the second most common. Kaspari and Joern (1993) reported similar results for Grasshopper Sparrows in Nebraska. They also examined the food habits of adult Grasshopper Sparrows and found that adults fed more on seeds and beetles than nestlings. Adults were also selective in the size of grasshoppers fed to nestlings with most being 15–35 mm in length (Kaspari and Joern 1993).

About 90% of the identified prey items fed to nestling Grasshopper Sparrows in our study were grasshoppers (68.1%) and insect larvae (22.6%). The energetic value of different arthropods is largely affected by their chitin content because chitin is largely indigestible (Karasov 1990, Klasing 1998). Larvae have a relatively low chitin content, while grasshoppers and other orthopterans have a much higher percentage of chitin (Kaspari 1991), and tend to have lower energetic value. Adult Grasshopper Sparrows minimize the chitin content of orthopteran prey delivered to nestlings by: (1) usually removing parts that contain the most chitin, such as legs (Kaspari 1990), and (2) usually feeding nestlings grasshoppers between 15 and 35 mm in length (Kaspari and Joern 1993, our study). This is likely
beneficial because smaller grasshoppers, relative to their mass, contain a greater percentage of chitin (Kaspari and Joern 1993) and provide less energy per unit of mass. Adult Grasshopper Sparrows may not prey on large grasshoppers (> 35 mm) because they may be too large for nestlings to consume, especially during the first few days post-hatching, and may require longer handling times (i.e., removing chitinous parts).

ACKNOWLEDGMENTS

We thank Ben Sutter and Chris Rutledge for assistance with the field work, C. E. Braun, Myles Falconer, and an anonymous reviewer for helpful comments, and the EKU research committee for financial support.

LITERATURE CITED


LARGE-SCALE MOVEMENT AND MIGRATION OF NORTHERN SAW-WHET OWLS IN EASTERN NORTH AMERICA

SEAN R. BECKETT1 AND GLENN A. PROUDFOOT1,2

ABSTRACT—We used information compiled by the U.S. Geological Survey's Bird Banding Laboratory and geographic information systems (GIS) analysis to identify trends in annual Northern Saw-whet Owl (Aegolius acadicus) movement across eastern North America. Analysis of 81,584 Northern Saw-whet Owl banding events revealed a southbound annual fall migration front with peak banding activity occurring progressively later in the season as latitude decreases. Northbound owls comprised <9% of owls banded and recaptured elsewhere in the same season, and <5% were recaptured northbound >100 km from banding location. There was no relationship between banding latitude and adult-to-juvenile ratio. However, the proportion of adults versus juveniles banded was not uniform among banding stations, suggesting age-differentiated migration patterns may exist. Information from multiyear foreign recaptures revealed that 72% of owls banded and subsequently recaptured at the same latitude in different years were recaptured <100 km from banding location. A similar trend was found in the Appalachian Mountains, the Great Lakes Basin, and the Atlantic seaboard. This indicates that Northern Saw-whet Owls may exhibit high migration route fidelity. These findings expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of aggregate data sets as a tool for answering large-scale questions regarding migration. Received 22 August 2010. Accepted 8 February 2011.

The Northern Saw-whet Owl (Aegolius acadicus) is a common but poorly-understood member of the North American forest fauna. Researchers first learned this species exhibited migratory behavior in 1906 when many washed up on the shores of Lake Huron after an autumnal storm (Saunders 1907). It is now widely recognized that large numbers of Northern Saw-whet Owls move south from breeding areas each fall, traveling as far south as Alabama, Louisiana, and northern Florida (Rasmussen et al. 2008). This autumn exodus is presumably undertaken to escape challenging winter conditions and to find a more stable resource base (Cheveau et al. 2004).

D. F. Brinker and colleagues created Project Owlnet (www.projectowlnet.org) to network a small group of banding stations in eastern North America. Project Owlnet has grown into a nationwide organization for coordinating and standardizing Northern Saw-whet Owl (NSWO) banding methodology. Currently, >125 NSWO banding stations allied with Project Owlnet monitor this species' migration annually (Huy 2010). These banding stations report time windows during which the majority of Northern Saw-whet Owls are caught in a season. These windows tend to occur later at southern stations than northern stations (Holroyd and Woods 1975, Weir et al. 1980, Brinker et al. 1997). Banding efforts have also revealed that some Northern Saw-whet Owl populations have cyclical migration irruptions about every 4 years. These irruptions are likely due to periods when prey abundance is followed by scarcity, implied by exceptionally high numbers of Northern Saw-whet Owls captured in the fall compared to 'normal' years (Davis 1966, Brinker et al. 1997, Whalen and Watts 2002, Brittain et al. 2009). Banding information has begun to illuminate age-differentiated migration trends in Northern Saw-whet Owls. Juvenile owls may migrate earlier than adults in some areas, and the age ratio of banded owls varies greatly among years and locations (Paxton and Watts 2000, Stock et al. 2006, Brittain et al. 2009).

Our knowledge of Northern Saw-whet Owl migration is clearly limited by the scale of previous research. Virtually all publications have been local or regional, often analyzing data from one or two banding stations. The only study in eastern North America using data from >six stations is 36 years old and limited by the number and distribution of banding stations available at that time (Holroyd and Woods 1975). Over 160,000 Northern Saw-whet Owls have been banded since Holroyd and Woods (1975) published their findings. This rigorous banding effort has generated an extensive data base archived at the U.S. Geological Survey’s Bird Banding Laboratory (BBL) that has remained unexplored in eastern North America.

Our objectives were to use the BBL data base to explore multiple questions. (1) Does the timing and direction of the migration front reported in regional studies exist across eastern North Amer-
ica? (2) Do Northern Saw-whet Owls exhibit inter-annual migration-route fidelity? (3) Do large-scale age-differentiated movement patterns exist? Answering these questions at this novel scale will expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of collective data sets.

METHODS

Data Source, Study Area, and Data Preparation.—We assessed movement patterns using the BBL data base of 170,468 Northern Saw-whet Owl banding events and 2,741 reports of subsequent encounters with banded owls (hereafter, recapture will be used for owls encountered post-banding, dead or alive). We examined information from 81,584 Northern Saw-whet Owls banded in 1999–2008 during fall migration between 1 September and 31 December. We assumed this parsing would ensure that nearly all records represented migrating owls. Excluding pre-1999 records ensured that most owls were banded using the audio lure mist-netting technique described in Erdtmann and Brinker (1997). Records exist across North America, but data west of the Mississippi River are geographically disparate and small in sample size. Thus, we restricted the analyses to records from eastern North America.

Data Analysis.—The BBL reports banding events as either the exact latitude and longitude of the banding location, or the corner coordinates of the 10-minute or 1-minute block that a station falls within. The data base does not report station or bander names, so it is not possible to match all banding event coordinates exactly to banding stations indicated by Project Owlnet (Huy 2010). Thus, we define a banding station as any coordinate where at least one Northern Saw-whet Owl was banded. A 10-minute block is ≈20 km wide, so the variation in banding coordinate precision is negligible at the scale of eastern North America.

We used a geographic information system (GIS) to draw vectors between banding and recapture locations for each individual captured multiple times, and calculated the spherical lengths of each vector. Compass bearings for each vector were calculated using a Standard Mercator projection designed to represent the line between any two points on a sphere as a constant azimuth. Vectors do not necessarily follow the migration path, but are sufficient for understanding overall distance and direction-of-travel between banding and recapture locations. All spatial analyses were performed using ArcView 9.3® (ESRI 2008).

Migration Timing.—We subdivided eastern North America into lateral bars 01° latitude in width (Fig. 1). We aggregated all banding events by these bars and calculated the mean Julian banding day at each bar. The 01° bars were chosen for convenience and were sufficiently wide to each contain a representative number of banding events. We verified that the mean banding day at each latitude bar coincided with a peak in migration activity represented by a bell curve in frequency distribution of banding days. There was a unimodal Gaussian distribution at all except four latitude bars south of Virginia. These four bars were ultimately excluded from analysis due to small sample size. Mean banding day was graphed against latitude bar, and against the latitude of banding stations with >50 banding events. We used linear regression to assess the strength of these relationships. Similar analyses were conducted to assess differences between adult and juvenile owl movements. Mean banding days for each latitude bar were compared using Chi-square contingency tables. All analyses performed using 01° latitude bars were also performed in the same manner and over the same area using 01° longitude bars to simultaneously identify east-west movement patterns.

We modeled migration timing in eastern North America by performing surface interpolations based on mean banding days at banding stations with >50 banding events. The model used inverse-distance weighting (ESRI 2008) of mean banding days at stations within a fixed-distance neighborhood around each predicted raster cell defined as an ellipse of 1.5° latitude and 05° longitude in radius (power = 1). The search neighborhood was restricted in latitude to limit bias of stations unevenly distributed far north or south of a given cell. The search neighborhood longitude was selected to restrict influence of distant stations while being sufficiently inclusive to interpolate the entire surface.

Variation in banding effort among stations cannot be calculated with the BBL data base. We normalized for banding effort where possible by comparing proportional values among stations rather than using raw totals, or aggregating data by latitude bar instead of banding station.

We estimated migration speed by plotting distance between banding and recapture over time.
for Northern Saw-whet Owls captured twice in the same season. We used the slope of the line-of-best-fit to approximate average speed.

Route Fidelity.—We predicted a species with high migration route fidelity would demonstrate low longitudinal deviation with respect to seasonal latitudinal position, i.e., the longitude at which an owl crosses a given latitude during migration would be similar among years. The longitudinal distance between the two locations would represent route deviation. Thus, if migrating owls maintain high route fidelity, they should not be recaptured long distances east or west within a single latitude bar from banding location. Longitudinal deviation and recapture records have been used for assessing migration route fidelity in other species (Rimmer and Darmstadt 1996, Alerstam et al. 2006). Thus, we chose to examine migration route fidelity by isolating from the data base all owls recaptured within 0.5° latitude of their banding location at least 1 year after banding. We consider a 0.5° latitude window sufficiently conservative to accurately represent route deviation while controlling for spurious influence of latitudinal position, i.e., we assume longitudinal route position may change with latitudinal
movement; the narrower the latitude bar the more reliable the assessment. We ascertained overall route fidelity by examining the frequency distribution of the banding-to-recapture distance for each owl. We explored general regional differences in route fidelity by analyzing fidelity separately for owls banded in the Great Lakes Basin, the Appalachian Mountains, and the Atlantic seaboard. These regions are defined inexact (Fig. 1), but are sufficient for making broad comparisons in Northern Saw-whet Owl movements among regions. We used Chi-square contingency tests to ascertain if differences in fidelity exist among regions or among regions and all owls.

Migration Direction.—We generated rose diagrams (Kovach Computing Services 2010) to calculate the mean azimuth and angular distribution of all banding-to-recapture vectors of Northern Saw-whet Owls captured at different stations in the same migration season. Additional rose diagrams were generated that considered owls recaptured >100 or >500 km from banding location to assess the possible influence of owls being recaptured disproportionately among proximate stations (thereby influencing overall angular distribution). We analyzed regional differences in directionality by isolating owls banded around the Great Lakes Basin, in the Appalachian Mountains, or along the Atlantic seaboard and recaptured >100 km from banding location (Fig. 1). We compared the mean directionality among these groupings using pair-wise Watson-Williams F-tests described in Fisher (1993).

Age-differentiated Migration.—We tested whether spatial differences exist between adult and juvenile movement patterns. We aggregated banding events into 0.5° latitude bars and calculated the age ratio of the owls within each bar. Linear regressions were used to assess the strength of the relationship between age ratio and latitude bar. This was done across all years (1999–2008) and independently for each year to reveal differences in movement patterns between irruption and non-irruption years.

We examined spatial differences in migration by performing a surface interpolation of the age ratio of Northern Saw-whet Owls at banding stations with >50 banding events. The interpolations used inverse-distance weighting (ESRI 2008) of age ratios at banding stations within a 3° search radius around each predicted raster cell (power = 2). This search neighborhood restricts the influence of distant stations while being sufficiently inclusive to interpolate the entire surface. This was done for all owls and separately for irruption and non-irruption years. We compared mean banding latitude by age class of all migrating Northern Saw-whet Owls using Wilcoxon Rank-Sum tests. This was done with pooled data (1999–2008) and separately by years.

We examined whether proportions of adults versus juveniles differed among years using Chi-square contingency tests, followed by a post-hoc analysis of means for proportions to identify which years were significant deviants (SAS Institute Inc. 2010).

RESULTS

We reviewed information on 81,584 Northern Saw-whet Owls banded in eastern North America during fall migration (1 Sep to 31 Dec) 1999–2008. Banding information was provided by 356 banding stations, 132 of which reported >50 banding events. Twenty stations reported 58% of all banding events (Fig. 1). Forty-five percent of the 81,184 banding events (of 81,584 total) with assigned age were adults and 55% were juveniles. There were 2,184 owls recaptured during fall migration. Seventy-three (3.3%) of these were recaptured >1,000 km from the original banding site.

Migration Timing.—There was a clear trend of northern banding events occurring earlier in the migration season than southern banding events (Fig. 2). The mean ± SD banding day at each latitude bar was 3.8 ± 2.7 days later than the bar immediately north of it. Mean banding day was not significantly different at any latitude bar among juveniles, adults, and all Northern Saw-whet Owls ($\chi^2_{22} = 0.03, P > 0.95$). The average difference between adult and juvenile mean banding day at each latitude was 1.2 days (range = 0.17–2.88). Surface interpolation of predicted mean banding day revealed a similar north-south trend with earlier means occurring consistently farther north than later means (Fig. 3). The earliest mean banding days were predicted for eastern Ontario and Quebec, and progressed gradually southward. The latest mean banding days were in Virginia, Delaware, West Virginia, and Indiana, although the interpolation was not performed farther south due to the lack of banding stations and few records in that region.

Northern Saw-whet Owls moved ~10.5 km per night on average (Fig. 4). The line-of-best-fit of mean migration speed was drawn using owls
banded and recaptured ≤33 nights apart because there were insufficient same-season recapture data >33 days to accurately represent migration speed at longer time intervals.

Migration Route Fidelity.—Seventy-two percent of 512 Northern Saw-whet Owls whose route deviation could be assessed (recaptured >1 year after banding within 0.5° latitude of banding location) were recaptured within 100 km east-west of their banding location. Thirty-four percent were recaptured within 20 km. The individual deviating farthest from its previous migration route was recaptured 981 km from its banding location. Forty-one percent of the data was represented by individuals banded and recaptured at two proximate stations west of Lake Michigan. We removed individuals encountered at these stations to isolate their effect on the overall analysis. The difference in results was statistically significant (χ² = 30.34, P < 0.001); however, removal of these stations resulted in an increase in route fidelity (Table 1).

There was no significant difference in route fidelity measures among owls banded in the Great Lakes Basin, Appalachian Mountains, and Atlantic seaboard regions (χ² = 9.08, P = 0.33, Table 1). There were no significant pair-wise differences between all owls and regional groupings (χ² < 8.16, P > 0.09).

Migration Direction.—Mean ± SD vector azimuth of 688 Northern Saw-whet Owls banded and recaptured at different locations during the same fall migration was 191.5 ± 3.8° and statistically similar (F₁ = 0.16, P = 0.689) to owls banded and recaptured >100 km apart (Fig. 5A, B). Significantly different (F₁ = 13.74, P < 0.001) south-southeastern movement was found in owls banded and recaptured >500 km apart (Fig. 5C). Eight percent (8.2%) of owls banded and recaptured at different locations were recaptured north of where they were banded; 4.4% of northbound owls were recaptured >100 km from banding location, and none was recaptured >500 km distant.

There was a significant difference in directionality among all owls recaptured >100 km from banding site and all three regional groupings (F₁ > 4.26, P < 0.04, Fig. 5B, D-F). There was a significant difference in mean directionality among owls banded in the Great Lakes Basin versus those banded in the Appalachian Mountains (F₁ = 11.54, P < 0.001 Fig. 5D, E) and the Atlantic seaboard (F₁ = 25.00, P < 0.001, Fig. 5D, F). There was no difference in mean directionality among owls banded in the Appalachian Mountains region and the Atlantic seaboard region.

Age-differentiated Migration.—Proportions of adults versus juveniles differed significantly among years (χ² = 5.071.01, P < 0.0001). Years 1999, 2001, 2003, 2006, and 2007 were significant deviants below the overall mean proportion. All other years were significant deviants above the overall mean proportion (Table 2).
Predicted mean banding day

- 271 - 287
- 288 - 294
- 295 - 299
- 300 - 304
- 305 - 310
- 311 - 338

Banding station with > 50 banding events

FIG. 3. Predicted fall migration timing of Northern Saw-whet Owls across eastern North America based on mean banding day at 132 stations with >50 banding events, 1999–2008. Calculated by inverse-distance weighted interpolation that considers stations within a 1.5° latitude and 05° longitude radius ellipse around each raster cell. Reference Julian dates: 1 October = 274; 1 November = 305. Dashed lines represent interpolation boundary.

FIG. 4. Mean ± SD (solid diamonds) and maximum distance (hollow diamonds) traveled by 915 Northern Saw-whet Owls recaptured x days after banding. The solid line-of-best-fit shows the trend in mean distance traveled from 0 to 33 days (\( y = 10.5x + 47.7, r^2 = 0.85, P < 0.001, n = 825 \)). The dashed line-of-best-fit shows the trend in mean distance traveled from 34 to 85 days (\( y = -3.3x + 562.7, r^2 = 0.03, P = 0.28, n = 90 \)). Separate trend lines were presented to reveal that the time-distance association appears to break down after ~33 days.
Beckett and Proudfoot • NORTHERN SAW-WHET OWL MIGRATION

TABLE 1. Migration route deviation in Northern Saw-whet Owls recaptured within 0.5° latitude from banding location >1 year after banding. ‘Distance’ represents straight-line distance between banding and recapture locations. A large proportion of same-site recaptures occurred at two sites west of Lake Michigan. We present a truncated data column that does not include information from these two sites to examine their effect on the overall trend. Further information is presented for owls banded within specific regions. The two sites west of Lake Michigan are excluded from the ‘Great Lakes’ group.

<table>
<thead>
<tr>
<th>Distance (km)</th>
<th>All owls (n = 512)</th>
<th>Truncated data (n = 312)</th>
<th>Great Lakes (n = 161)</th>
<th>Appalachian Mountains (n = 41)</th>
<th>Atlantic seaboard (n = 50)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
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<tr>
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<td>4.9</td>
<td>21</td>
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<td>14</td>
</tr>
</tbody>
</table>

There was no significant relationship between adult: juvenile ratio and latitude for all years combined (n = 81,184, r² = 0.008, P = 0.77, Fig. 6). The relationship was significant in irruption year 2003 and non-irruption years 2006 and 2008, when tested separately by year. The relationship was insignificant and in inconsistent directions in 7 of 10 years (Table 3). There was no significant difference in adult versus juvenile mean banding latitude for all years combined (P = 0.46, Table 2). There was a significant difference in 9 of 10 years when tested separately, but the differences were not in a consistent direction.

Surface interpolation of age ratios showed areas of predicted high and low values (Fig. 7), but these areas were patchy and localized. Highest adult: juvenile ratios were predicted in Wisconsin, Virginia, northern New England, and New York. Lowest adult: juvenile ratios were predicted in eastern Ontario north of Lake Huron, eastern Quebec, around Lake Erie, and coastal stations in Massachusetts, Rhode Island, New Jersey, and around Chesapeake Bay (Fig. 7A). Results were similar in irruption years (Fig. 7B), but with lower overall ratios across the surface. Results for non-irruption years were similar to the interpolation for all owls (Fig. 7C), but with highest adult: juvenile ratios also occurring across Virginia, West Virginia, Kentucky, and Indiana.

DISCUSSION

Migration Timing.—Peak migration activity occurred progressively southward over the course of the season, suggesting that Northern Saw-whet Owls migrate in distinct fronts. This trend is consistent using multiple analyses, indicating the strength of this trend and the reproducibility of the results (Figs. 2–3). This supports the southbound trend that researchers have supposed for decades based on the accretion of regional observations (Mueller and Berger 1967, Weir et al. 1980, Erman et al. 1997, Brittain et al. 2009). We could expect a less-striking latitudinal gradient and more irregular distributions of the owls banded at each latitude if Northern Saw-whet Owls were moving southward haphazardly over the entire migration season. The observed trend implies that fall migration is uniform and not a random seasonal dispersal in search of better resources.

Our results closely match those of Holroyd and Woods (1975), the only other study that compares mean Northern Saw-whet Owl capture dates among multiple banding stations in eastern North America. The distribution of banding dates for most of their study regions were within our predicted means (Fig. 3). Our predicted means for Massachusetts, Maryland, and New Jersey were 1–2 weeks later than indicated in Holroyd and Woods (1975). Mean banding day in Ontario was predicted ~1 week earlier than they indicated. This inconsistency may be due to varying weather patterns, shifts in population centers that change migration distances or the small sample size (n = 4,802) available for their study. The overall similarity in results despite the >30 year difference in sampled populations (1955–1969 in theirs vs. 1999–2008 in ours) shows the long-term temporal consistency of this species’ fall migration. This similarity also shows these results may be reproducible using other methodologies. The abrupt late mean banding day predicted in central Illinois may be explained by low banding station density in that area. This area may reveal
FIG. 5. Directional movement of Northern Saw-whet Owls in eastern North America during fall migration, including mean compass bearing and 95% confidence interval (indicated by black line and cross-bar), 1999-2008. Rose wedge lengths and axis labels indicate percentage of total within that azimuth bin. A = the angular distribution of banding-to-recapture vectors of 688 Northern Saw-whet Owls banded and recaptured in the same season (mean = 191.5 ± 3.8°). B = distribution of 549 owls recaptured >100 km from banding location (mean = 190.4 ± 3.8°). C = distribution of 87
TABLE 2. Adult and juvenile proportions by year (1999-2008), and one-way analysis of mean adult banding latitude versus mean juvenile banding latitude of Northern Saw-whet Owls in eastern North America (Wilcoxon Rank-Sum tests).

<table>
<thead>
<tr>
<th>Year</th>
<th>Adult n (%)</th>
<th>Juvenile n (%)</th>
<th>Mean ± SE adult banding lat. N</th>
<th>Mean ± SE juvenile banding lat. N</th>
<th>Wilcoxon Z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>3,378 (32)</td>
<td>7,298 (68)</td>
<td>43.33 ± 0.05</td>
<td>42.56 ± 0.04</td>
<td>11.83</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2000</td>
<td>3,553 (60)</td>
<td>2,320 (40)</td>
<td>44.10 ± 0.04</td>
<td>44.63 ± 0.05</td>
<td>8.27</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2001</td>
<td>2,929 (41)</td>
<td>4,067 (59)</td>
<td>43.33 ± 0.05</td>
<td>42.50 ± 0.05</td>
<td>12.61</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2002</td>
<td>3,220 (53)</td>
<td>2,894 (47)</td>
<td>43.76 ± 0.04</td>
<td>44.24 ± 0.05</td>
<td>6.21</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2003</td>
<td>3,686 (40)</td>
<td>5,590 (60)</td>
<td>43.75 ± 0.09</td>
<td>44.22 ± 0.04</td>
<td>8.27</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2004</td>
<td>4,743 (58)</td>
<td>3,449 (42)</td>
<td>43.36 ± 0.04</td>
<td>43.73 ± 0.05</td>
<td>12.61</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2005</td>
<td>4,268 (51)</td>
<td>4,060 (49)</td>
<td>44.19 ± 0.04</td>
<td>44.18 ± 0.05</td>
<td>0.26</td>
<td>0.79</td>
</tr>
<tr>
<td>2006</td>
<td>2,645 (37)</td>
<td>4,540 (63)</td>
<td>44.69 ± 0.05</td>
<td>45.47 ± 0.04</td>
<td>13.12</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2007</td>
<td>4,533 (32)</td>
<td>9,659 (78)</td>
<td>43.27 ± 0.04</td>
<td>43.16 ± 0.03</td>
<td>2.28</td>
<td>0.02</td>
</tr>
<tr>
<td>2008</td>
<td>3,267 (75)</td>
<td>1,076 (25)</td>
<td>43.26 ± 0.05</td>
<td>44.70 ± 0.09</td>
<td>12.20</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Totals</td>
<td>36,231 (45)</td>
<td>44,985 (55)</td>
<td>43.67 ± 0.02</td>
<td>43.69 ± 0.02</td>
<td>-0.74</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Limitations in all interpolation modeling to predict values in regions with few or no sampling points. Banders may begin trapping in response to reports through Project Owlnet of banding success at more northern stations. Thus, the calendar of Northern Saw-whet Owl banding events in this study may conceivably be influenced by Project Owlnet, and this influence may bias the results. However, we observed a Gaussian distribution of banding events at each latitude bar (Fig. 2) demonstrating that a sufficient sampling of owl movement is achieved despite the potential timing biases associated with Project Owlnet communication. We suspect most banders anxiously wait for migration to begin each season and open nets well before more-than-expected numbers arrive, e.g., ~1-2 owls/night. If anything, Project Owlnet improves the accuracy of our seasonal timing assessment.

The average speed (10.5 km/day, Fig. 4) was slower than the speed of individuals reported in other studies (14-32 km/day in Virginia, Brinker et al. 1997; 20-30 km/day in Wisconsin, Erdman et al. 1997; 28.8 km/day in Indiana, Brittain et al. 2009; 37 km/day in Alberta, Priestley et al. 2010). However, if we assume that each degree of latitude in our study is ~111 km, the progression of the peak banding window (Fig. 2) indicates the migration 'front' moves ~30 km/day. The discrepancy between these two rates may be because the migration 'front' is a measure of fluid population movement, while the migration speed analysis (Fig. 4) represents individual movements including stopovers (Whalen and Watts 2002) not reflected in the measurement of overall population movement. The fastest records (Fig. 4) demonstrate that Northern Saw-whet Owls are capable of sustained movement even if normal migration behavior includes frequent stopovers.

Migration Route Fidelity.—Catry et al. (2004) argue that migrant passerines rarely exhibit route and stopover-site fidelity because they are solitary, short-lived, and highly terrestrial (and therefore have more potential stopover sites than other types of birds). Their energetically costly flight style also hinders correction for wind drift. These qualities are true for Northern Saw-whet Owls as well, but our findings suggest this species may be generally faithful to migration routes. Seventy-two percent of owls recaptured >1 year after banding ±0.5° latitude from banding location were recaptured <100 km from their banding locations (Table 1), suggesting that individuals follow similar migration routes among years.

The Great Lakes may characterize geographic barriers that could constrict Northern Saw-whet Owl movement and cause a migratory bottleneck.
This type of funneling may explain why 41% of owls in our fidelity analysis were banded and recaptured at two stations west of Lake Michigan. It may be argued this potential geographic funneling biases fidelity estimates. However, similar circumstances of restricted movement would be required throughout the year to challenge migration route fidelity estimates. Clearly, there was ample opportunity for these individuals to move southward along the other side of the lake or to take a different route void of the Great Lakes influence. Consistent repeated movement along the same corridor during fall migration, constricted or not, is a valid assessment of route fidelity. It is possible that some owls encountered at these two sites were residents, but similar fidelity measures were found in the Great Lakes Basin when these stations were removed, and in regions where few resident owls are present (Rasmussen et al. 2008). The lack of significant difference in fidelity measures among the Great Lakes Basin and other regions suggests that geologic constraints do not fully explain the high route fidelity indicated by our analysis. High fidelity was observed in the Appalachian Mountains where movement is unlikely restricted by geologic features, but may be selected for structural and resource benefits, showing that Northern Saw-whet Owls may follow consistent routes where geographic bottlenecks are not present.

Our study addresses migration route fidelity rather than nesting-site fidelity, but our results contribute to the ongoing discussion of nomadic behavior in Northern Saw-whet Owls (Marks and Doremus 2000, Bowman et al. 2010).

### TABLE 3. Linear relationship between adult-to-juvenile ratio (y) and latitude bar (x) for Northern Saw-whet Owls in each year, 1999-2008.

<table>
<thead>
<tr>
<th>Year</th>
<th>y =</th>
<th></th>
<th>F</th>
<th>df</th>
<th>P</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>0.009x + 0.012</td>
<td>0.027</td>
<td>0.277</td>
<td>11</td>
<td>0.61</td>
<td>10,676</td>
</tr>
<tr>
<td>2000</td>
<td>-0.146x + 8.124</td>
<td>0.268</td>
<td>3.657</td>
<td>11</td>
<td>0.085</td>
<td>5,873</td>
</tr>
<tr>
<td>2001</td>
<td>0.037x - 0.894</td>
<td>0.118</td>
<td>1.335</td>
<td>11</td>
<td>0.275</td>
<td>6,995</td>
</tr>
<tr>
<td>2002</td>
<td>-0.054x + 3.386</td>
<td>0.233</td>
<td>3.04</td>
<td>11</td>
<td>0.112</td>
<td>6,114</td>
</tr>
<tr>
<td>2003</td>
<td>-0.042x + 2.473</td>
<td>0.414</td>
<td>7.066</td>
<td>11</td>
<td>0.024</td>
<td>9,276</td>
</tr>
<tr>
<td>2004</td>
<td>-0.026x + 2.542</td>
<td>0.058</td>
<td>0.617</td>
<td>11</td>
<td>0.45</td>
<td>8,192</td>
</tr>
<tr>
<td>2005</td>
<td>0.019x + 0.280</td>
<td>0.066</td>
<td>0.712</td>
<td>11</td>
<td>0.419</td>
<td>8,328</td>
</tr>
<tr>
<td>2006</td>
<td>-0.039x + 2.373</td>
<td>0.348</td>
<td>5.950</td>
<td>10</td>
<td>0.037</td>
<td>7,185</td>
</tr>
<tr>
<td>2007</td>
<td>0.027x - 0.556</td>
<td>0.076</td>
<td>0.826</td>
<td>11</td>
<td>0.385</td>
<td>14,202</td>
</tr>
<tr>
<td>2008</td>
<td>-0.766x + 36.943</td>
<td>0.740</td>
<td>29.770</td>
<td>11</td>
<td>0.0003</td>
<td>4,343</td>
</tr>
</tbody>
</table>
FIG. 7A = predicted age distribution of migrating Northern Saw-whet Owls in eastern North America, 1999–2008, based on age ratios at 132 stations with >50 banding events. 7B = predicted age distribution of owls at 89 stations in irruption years. 7C = predicted age distribution of owls at 101 stations in non-irruption years. Interpolation uses inverse-distance weighting of adult: juvenile ratios at banding stations within a 3° radius around each predicted raster cell. Dashed lines represent interpolation boundary.

analysis indicated that many owls are banded in high-latitude breeding regions and recaptured nearby in subsequent years. This suggests that some owls may consistently travel from historical breeding areas and maintain high migration route fidelity. For example, if a bird is repeatedly captured at the same site in Wisconsin in different years during migration, it is more likely to have bred repeatedly in the western Great Lakes Basin than in eastern Quebec. Thus, although Northern Saw-whet Owls may only rarely reoccupy the same breeding territory (Marks and Doremus 2000), they may still remain regionally faithful.

Marks and Doremus (2000:302) noted "the best evidence for nomadism would be the capture of marked individuals at widely separated breeding sites in different years," yet a decade later there is still limited banding effort during the breeding season, and insufficient data to fully understand the scale of nomadism in Northern Saw-whet Owls. We conclude, based on the level of migration route fidelity found in this study, this species has ordered movement during migration and is not moving haphazardly in search of food.

Migration Direction.—Our results show a clear southbound movement pattern indicated by the directional distribution of Northern Saw-whet Owls banded and recaptured in the same migration season (Fig. 5). Most studies assume a southward migration based on the accumulation of southbound movement via recapture reports in their study areas (Brinker et al. 1997, Erdman et
al. 1997, Brittain et al. 2009), but this is the first study to quantify the directionality of fall migration in this species using large-scale recapture data.

The results also reveal the frequency of northbound movement. Local studies emphasize northbound individuals when summarizing recapture information (Holroyd and Woods 1975, Erdman et al. 1997, Marks and Doremus 2000), and this may give the impression the overall migration direction is more random. However, northbound individuals comprise a small percentage of same-year recaptures (Fig. 5). Fall movements in non-southbound directions should be considered exceptions to the general southward migration trend. The similar southward mean azimuths and narrow confidence intervals, regardless of minimum banding-to-recapture distance (Fig. 4B, C), suggests that most directional distribution biases due to encounters among proximate stations are overwhelmed by actual movement patterns.

The uniform directionality distribution of Northern Saw-whet Owls in the Atlantic seaboard region may indicate that migration along the Atlantic seaboard is restricted by the coastline, and owls are following the coast rather than flying west into the Appalachian Mountains. The wider directional distribution of owls in the Appalachians suggest owls are moving somewhat more haphazardly in that region, possibly guided by the southwest orientation of the mountain range. This is congruent with observations in Alberta of Northern Saw-whet Owl movement guided by the Rocky Mountains and the boreal forest edge (Priestley et al. 2010). This less-uniform migration may be due to the extensive forest cover across the Appalachian range, or due to owls searching for suitable wintering areas after reaching the winter range.
The wide directionality distribution of migrants in the Great Lakes Basin illustrates that owls traveling through this region have many directional options, supporting our conclusions of high route-fidelity in this region (Table 1).

Overall observed directionality may be influenced by the distribution of banding stations across eastern North America. For example, owls migrating southeast from western Pennsylvania would be more represented in the data base than owls migrating southwest due to the location and number of ‘downstream’ stations (Fig. 1). Station location biases may explain the significant difference in directionality between owls recaptured >100 versus >500 km from banding location. However, such biases do not obscure our general conclusion that Northern Saw-whet Owls are migrating predominately southward.

Age-differentiated Migration.—Juveniles were banded more frequently than adults, and this is consistent with local studies (Weir et al. 1980, Stock et al. 2006, Brittain et al. 2009). Banders in eastern North America report a striking increase in the proportion of juveniles banded in irruption years (Brinker et al. 1997, Paxton and Watts 2000, Whalen and Watts 2002). Our results support this finding. The percentage of adult Northern Saw-whet Owls was lowest in 1999 and 2007, two well-recognized irruption years, and highest in years immediately following these irruptions (Table 2). This is consistent with local findings as well (Paxton and Watts 2000). The discrepancy in proportions of juveniles is likely due to the cyclical prey base causing high reproductive success in irruption years followed by poor success the following year (Cheveau et al. 2004). Also, many adults in post-irruption years are returning second-year birds that hatched the previous year.

Our results did not reveal unequivocal evidence of age-differentiated migration based on latitude.
or longitude. Areas of both high and low adult: juvenile ratios occur in the northern and southern extents of our analyses (Fig. 7). The lowest adult: juvenile ratios were in the two northernmost latitude bars, but the highest ratios were in the next three adjacent bars (Fig. 6). By-year regression analysis showed no consistent relationship between age ratio and latitude. Only 3 of 10 years tested had a significant trend, and these were not in a uniform direction (Table 2). Tests of mean banding latitude by age were not significant for all years, and they were not in a uniform direction (Table 3). The direction or significance of these tests is not explained by irruption or non-irruption years. The small mean difference in migration timing between adults and juveniles at each latitude bar does not suggest differential migration timing by latitude.

We did not detect movement patterns explained by latitude, but our interpolations indicate that adult versus juvenile migration is non-uniform across eastern North America (Fig. 7). Juveniles in Idaho had lower body condition scores than adults (Stock et al. 2006). Along the Atlantic Coast, juveniles may arrive on the Delmarva Peninsula almost 2 weeks earlier than adults (Paxton and Watts 2000). Juveniles also benefit less from site familiarity than their parents, and may be less inclined to remain near breeding areas (Côté et al. 2007). These studies imply age-related differences in the ability to cope with challenging conditions, and suggest that juveniles may migrate differently than adults in some areas as a result.

The predicted areas of high and low adult: juvenile ratios were similar in both irruption and non-irruption years and support the hypothesis of age-specific preferences for migration routes or wintering sites (Fig. 7B, C). Regionally variable forest structure, prey availability, or climate may influence these preferences, and may explain the patchiness observed in our interpolations. It is possible that resident populations of Northern Saw-whet Owls at high latitudes or high elevations in the Appalachian Mountains are influencing these interpolations (Rasmussen et al. 2008). However, the migration timing interpolation (Fig. 3) and directionality analyses (Fig. 5) showed no clear evidence of resident owls obscuring the overall observed migration pattern, suggesting the impact of residents on the overall data set is minimal.

The quality of any interpolation is limited by the accuracy and distribution of sampling points across the surface. Thus, we refrain from interpreting interpolation results in areas with low station density or areas influenced heavily by one data point. Increased banding efforts in regions with low station density will greatly improve our understanding of large-scale migration patterns in this species.

This study is an example for assessing the strength and versatility of using the BBL's large banding data base to understand bird migration. The kinds of information that can be gleaned from banding studies may be limited compared to other techniques, but banding is one of the only tools available for studying cryptic or nocturnal species like Northern Saw-whet Owls. We expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of aggregate data sets as a tool for answering large-scale questions regarding migration by assessing movement patterns beyond published regional trends.

ACKNOWLEDGMENTS

We thank M. A. Cunningham of the Department of Earth Science and Geography at Vassar College for support in designing the analyses. This project would not have been possible without data generated by hundreds of Northern Saw-whet Owl banders who submit their information to the USGS Bird Banding Laboratory; information provided by D. F. Brinker of Project Owlen, David Okines of Prince Edward Point Bird Observatory, David Evans of the Hawk Ridge Nature Reserve, Eugene Jacobs of Linwood Springs Research Station, Jon McCracken of Thunder Cape Bird Observatory, Bruce Murphy of Hilliardton Marsh, and Scott Weidensaul of The Ned Smith Center for Nature and Art account for 47% of all banding data used in this study. We thank Jennifer Pontius of the University of Vermont for support in statistical analysis. Logistical support was provided by Daniel Bystrak of the Patuxent Wildlife Research Center and associates of Project Owlen. We thank the Vassar College Environmental Research Institute for financial support of the project.

LITERATURE CITED


Beckett and Proudfoot • NORTHERN SAW-WHET OWL MIGRATION


DISTRIBUTION OF MIGRATORY LANDBIRDS ALONG THE NORTHERN LAKE HURON SHORELINE

DAVID N. EWERT,1,7 MICHAEL J. HAMAS,2,3 ROBERT J. SMITH,4,19 MATT E. DALLMAN,2,5 AND SCOTT W. JORGENSEN6

ABSTRACT.—The distribution of landbirds during migration in forested landscapes of eastern North America is poorly known. We describe (1) the distribution of landbirds in northern white cedar (Thuja occidentalis) dominated forests as a function of distance from northern Lake Huron in Michigan during spring and autumn migration, and (2) discuss factors that may affect the distribution of these migrants. Both long- and short-distance migrants in spring and fall were concentrated within 0.4 km of the Lake Huron shoreline. This pattern was particularly pronounced during spring when aquatic-hatched insects such as midges and their predators (e.g., spiders) are most common and occur in largest numbers near the shoreline. Both long- and short-distance migrant abundance was associated with midge abundance, controlling for date, during spring migration but not during fall migration. Migrants may concentrate near the shoreline because of the barrier effect of Lake Huron and relatively abundant food resources, especially during spring migration. Terrestrial habitats adjacent to bodies of water, where aquatic-dependent invertebrates are relatively abundant may provide important stopover sites for landbird migrants. Our results suggest coastal areas within the Great Lakes region provide critical stopover habitat for landbird migrants and should be a focus of conservation efforts, especially given the increasing development pressure that threatens these areas. Received 8 August 2009. Accepted 10 February 2011.

Migration is a high-risk, energetically costly event (Alerstam and Lindström 1990, Blem 1990) that is associated with relatively high mortality (Moore et al. 1995, Sillett and Holmes 2002), especially among young birds of the year (DeSante 1983, Ketterson and Nolan 1983). Landbirds use stopover sites during migration, which are areas where migrants rest, refuel, and seek shelter from predators and adverse weather conditions (Berthold 1975, Blem 1980, Alerstam and Lindström 1990, Moore et al. 1995). How migrants respond to stresses encountered is key to a successful migration. Thus, a network of stopover sites ranging from refugia with little food, such as islands or coastlines, to food rich sites may be needed by landbirds when migrating between breeding and wintering areas (Mehlman et al. 2005). Coastal stopover sites, including those adjacent to the Great Lakes, may be especially important to migrants because they may provide refugia and food resources to accumulate energy stores, both before and after crossing expanses of water (Moore et al. 1995; Dunn 2002; Smith et al. 2004, 2007; Bonter et al. 2007, 2009).

Recent work suggests shoreline areas adjacent to northern Lake Huron provide important stopover habitat to spring migrant landbirds (Seefelt 1997; Smith et al. 1998, 2004, 2007), possibly due to the presence of emergent aquatic midges (Diptera: Chironomidae). For example, at least two species of landbird migrants, Black-throated Green Warbler (Dendroica virens) and American Redstart (Setophaga ruticilla) foraged and used habitats differently, depending upon whether individuals were observed in shoreline habitats containing abundant midges or inland where few midges were observed (Smith et al. 1998, 2004). Smith et al. (2007) provided evidence that shoreline habitats within Michigan's eastern Upper Peninsula are resource rich during spring migration. Arthropod biomass estimates suggested more midges and spiders (Aranae: Archnidae) were present within shoreline habitats than inland and American Redstart foraging behavior reflected shoreline/inland differences in resource abundance (Smith et al. 2007). Furthermore, a suite of migrant species appeared to gain mass quickly in shoreline habitats during early spring, when midges and spiders were the predominant resource (Smith et al. 2007).

The Great Lakes strongly influence nearshore terrestrial habitats (Eichenlaub 1979, Albert et al.
species including paper birch (*Betula papyrifera*). and white pine (*Pinus strobus*), and deciduous *Picea glauca* (*Abies balsamea*). white spruce northern while cedar (*Thuja occidentalis*), balsam throughout the study area. Conifers, especially NEXRAD data (Bonter et al. 2009) suggests migrants concentrate along Great Lakes shoreline habitats during both spring and fall but we know little about the relative abundance of migrants along the shoreline and adjacent inland landscapes. No work has rigorously examined the influence of the northern Great Lakes on distribution of landbirds within the same landscape during both spring and fall migration. Our objective was to describe migrant landbird distribution along Great Lakes shoreline and the forest edge at the shoreline. Stations were aligned in transects perpendicular to the shoreline: we did not place stations on peninsulas to minimize potential biases associated with areas where migrants may concentrate. The center of each station was at least 50 m from the edge of secondary roads or open shoreline. We established stations in forest dominated by white cedar, balsam fir, paper birch, and quaking aspen to control for forest type. Appropriate stations at 3.2 km were not available in three cases due to inaccessibility, and we established stations at other nearby sites in appropriate habitat 3.2 km inland from the shoreline.

We recorded all birds detected by sight or sound at each station during 5-min count periods. We used 5- rather than 10-min counts to sample more sites and to ensure that individuals in rapidly moving flocks were counted only once. We conducted counts between sunrise and 1200 hrs EDT from 1 May to 5 June 1993 and 30 April to 5 June 1994, and from 16 August to 24 September 1993 and 15 August to 23 September 1994. Only a few early spring and late fall migrants, such as kinglets, Fox Sparrow (*Passerella iliaca*), and some icterids and cardueline finches largely migrated outside the sampling periods (D. N. Ewert, M. J. Hamas, and R. J. Smith, unpubl. data). We sampled all 45 points on each of the 10 count days each season. We surveyed birds across the entire study area every 3 to 5 days, dependent upon the weather. We did not conduct surveys during rain or high wind events. We assigned each observer a group of adjacent point count stations (to minimize travel and maximize sampling effort) the night prior to each survey. All observers sampled their assigned stations on the same day and no observer counted birds at the same station on two consecutive sampling dates.

We classified each bird species as a resident, or
short- or long-distance migrant (Gauthreaux 1991), and omitted resident species from the analysis. Migrants that breed north of the study area (northern breeders, Brewer et al. 1991), including (Philadelphia Vireo (Vireo philadelphi cus), Gray-cheeked Thrush (Catharus minimus), Tennessee Warbler (Oreothlypis peregrina), Orange-crowned Warbler (O. celata), Cape May Warbler (Dendroica tigrina), Palm Warbler (D. palmarum), Bay-breasted Warbler (D. castanea), Blackpoll Warbler (D. striata), Connecticut Warbler (0porornis agilis), Wilson’s Warbler (Wilsonia pusilla), and White-crowned Sparrow (Zonotrichia leucophrys), were analyzed independently from long-distance and short-distance migrants known to breed in the study area.

We were not able to distinguish individuals arriving to breed from those passing through our site en route to a more northerly or southerly migratory destination. This may confound interpretation of spatial distribution during both spring and fall migration. A comparison of banding records from spring migration to the breeding season for six species, Magnolia Warbler (Dendroica magnolia), Yellow-rumped Warbler (D. coronata), Black-throated Green Warbler, Blackburnian Warbler (X. fusca), Black-and-white Warbler (Mniotilta varia), and American Redstart captured in shoreline habitat within the same study area indicated that many more birds passed through the area than subsequently stayed to breed (R. J. Smith and F. R. Moore, unpubl. data). Local breeders comprised only a small percentage of the total captures during spring migration, and it is likely the spatial patterns observed in this group of species are valid.

We described forest composition at each point-count station using point-quarter sampling (Cottam and Curtis 1956). Description of the understory or shrub layer (shrubs were defined as <0.5 m tall and <2.5 cm diameter at breast height) was by counting all woody stems within a 10-m radius circular plot.

We tracked the phenological development of spring leaf-out and fall leaf-drop to estimate and
compare microclimatic differences between shoreline and inland areas, and potential food resources dependent on foliage. We collected phenology data following each 5-min bird survey on 10 paper birch and 10 quaking aspen trees nearest the center of the point-count station. Spring phenology was characterized as: (1) leaves in bud; (2) leaves emerging from bud (bud scales shed), (3) leaves unfurled but not fully expanded, and (4) leaves fully expanded. We categorized fall phenology as: (1) little or no loss of green leaves, (2) retention of >50% of leaves, some of which may have lost chlorophyll, (3) retention of <50% of leaves, some of which may have lost chlorophyll, and (4) loss of all leaves.

Midge abundance was visually estimated as the number of insects on vegetation and in the air within a 5-m radius circle from the center of the point-count circle. We quantified midge abundance during a 10-sec period following each bird count into one of four categories: (1) no midges, (2) 1-500 midges, (3) 501–1,000 midges, and (4) >1,000 midges. We did not collect data on other arthropod groups because we noted few other arthropods. Midge data were collected during spring and fall 1994 after it became evident birds were foraging on them in 1993, the first year of the study.

Statistical Analyses.—Distributions of relevant variables were examined for departures from normality and non-parametric statistics were used when transformations did not bring data into compliance with parametric testing assumptions (Zar 1996). Bird and midge count data were analyzed using SPSS 16.0 (SPSS 2008). We used general linear models (GLM) for natural log transformed data \(Y = \ln(X + 1)\), or GLM for ranked data followed by Tukey post hoc tests, Kruskal-Wallis Analysis of Variance, and Mann-Whitney tests (Conover 1999). We used Kendall partial rank-order correlations, a nonparametric method that eliminates the effect of a third variable on the relationships between the variables of interest, when necessary (Siegel and Castellan 1988).

Bird counts were modeled as a function of perpendicular distance from shoreline. We included transect as a factor in the analyses to control for effects of both longitude and individual transect, two potentially confounding variables. We included three temporal variables in each analysis: year, season, and date. Reported values are means ± SE.

RESULTS

Birds.—We recorded 2,577 observations of birds during the 2-year study (Appendix). Birds were most abundant near the shoreline for both long- and short-distance migrants (Fig. 2).

Spring.—Abundance of long-distance migrants was affected by year \(F_{1,808} = 21.01, P < 0.001\), distance from shore \(F_{4,808} = 11.06, P < 0.001\), transect \(F_{8,808} = 4.14, P < 0.001\), and date \(F_{13,808} = 72.40, P < 0.001\). Sites within 0.4 km of the shoreline had more birds than sites at distances greater than 0.4 km from the water (Fig. 2A). There was an immediate shoreline effect with more birds counted at the shoreline relative to all other distances except 0.4 km. There was no significant difference between number of birds observed at the immediate shoreline and birds counted at a distance of 0.4 km (Tukey \(P =\)
Species that breed north of the study area concentrated near the shoreline in spring (Fig. 3). There was an effect of year ($F_{1,1147} = 5.13$, $P = 0.024$), distance from the shoreline ($F_{4,809} = 10.44$, $P < 0.001$), and date ($F_{13,809} = 2.45$, $P = 0.003$) on number of northern breeders counted. A transect effect approached significance ($F_{8,809} = 1.90$, $P = 0.056$). More northern breeding birds were counted in shoreline habitat than at any other distance inland (Tukey $P < 0.001$; Fig. 3).

Abundance of spring short-distance migrants did not vary by year ($F_{1,807} = 0.242$, $P = 0.623$), but did vary by distance from shore ($F_{4,807} = 10.89$, $P < 0.001$), transect ($F_{8,807} = 5.21$, $P < 0.001$), and date ($F_{13,807} = 9.42$, $P < 0.001$). The immediate shoreline had more short-distance migrants than all other distances sampled (Tukey $P < 0.002$; Fig. 2A). There were no other differences in numbers of birds observed relative to distance from the shoreline (Tukey $P > 0.34$). Short-distance migrant abundance was associated with midge abundance after controlling for date ($t_k = 2.24$, $n = 420$, $P = 0.025$).

Abundance of fall short-distance migrants was not affected by year ($F_{4,1042} = 0.72$, $P = 0.40$) although it was influenced by distance from shoreline ($F_{4,1042} = 3.34$, $P = 0.010$; Fig. 2B), transect ($F_{8,1042} = 1.98$, $P = 0.046$), and date ($F_{15,1042} = 1.69$, $P = 0.047$). There were more short-distance migrants counted at the immediate shoreline than at other distances (Tukey $P < 0.040$), except 0.8 km (Tukey $P = 0.066$) and 3.2 km (Tukey $P = 0.071$). There were no other differences in number of birds observed relative to distance from the shoreline (Tukey $P > 0.070$). Fall short-distance migrant abundance was not associated with midge abundance after controlling for date ($t_k = -0.20$, $n = 420$, $P = 0.85$).

Abundance of fall short-distance migrants was not affected by year ($F_{1,1147} = 1.02$, $P = 0.31$) nor distance from the shoreline ($F_{4,1147} = 2.22$, $P = 0.064$) for species that breed north of the study area during fall migration. However, date ($F_{15,1147} = 1.95$, $P = 0.016$) and transect ($F_{8,1147} = 2.55$, $P = 0.009$) influenced number of transients counted during fall migration (Fig. 3). Abundance of northern breeders was associated with midge abundance after controlling for date ($t_k = 3.27$, $n = 420$, $P = 0.0014$).

Vegetation.—Forest composition was similar between shoreline and inland plots. The dominant tree in the study area, northern white cedar, had the same rank order in terms of importance value and density at both shoreline and inland sites (Table 1). Northern white cedar density was four
to 10 times greater than the other common species (balsam fir, quaking aspen, and paper birch).

Leaf emergence began on 6 May 1993 and 13 May 1994 and leaves were fully expanded at all stations by 30 May 1993 and 1994. The phenology of paper birch and quaking aspen was highly correlated ($r = 0.94, n = 1,052, P < 0.001$), and offset by a constant of 0.25 (aspen leaf out slightly preceded birch leaf out); thus, we averaged phenology scores for the two species to estimate phenology as a function of distance from the shoreline. Average phenological development during spring was later nearshore than inland ($F_{9,1075} = 29.10, P < 0.001$; Fig. 4). Average phenology was not a function of distance from the lake in autumn ($F_{4,425} = 0.247, P = 0.620$). Most leaves remained on the trees throughout the autumn migration period. Little leaf senescence (loss of chlorophyll) occurred during the fall sampling period.

Midges.—Spring midge abundance was significantly influenced by date ($F_{9,425} = 2.86, P = 0.003$), transect ($F_{11,425} = 2.25, P = 0.012$), and distance from shoreline ($F_{4,425} = 16.47, P < 0.001$). More midges were counted at the immediate shoreline than at all other distances (Tukey $P < 0.010$). There were no differences in number of midges counted between any of the other distances (Tukey $P > 0.764$; Fig. 5). Fall midge abundance was influenced by date ($F_{9,425} = 3.12, P = 0.001$) and distance from the shoreline ($F_{4,425} = 8.49, P < 0.001$), but not by transect ($F_{11,438} = 1.36, P = 0.189$). There were more midges observed at the immediate shoreline than inland (Tukey $P < 0.015$; Fig. 5). There were no differences in estimated midge abundance between any other distances.

FIG. 4. Average (± SE) aspen and birch phenology score by day along the northern Lake Huron shoreline. Inland encompasses all sampling points not at the immediate shoreline. Julian Day 130 = 10 May; Julian Day 150 = 30 May.

FIG. 5. Mean (± SE) midge abundance as a function of season and distance from the northern Lake Huron shoreline, 1993–1994.
The spatial difference in midge abundance was more than twice as large in spring as fall (Fig. 5). Phenology was unrelated to midge abundance after controlling for influence of date for both spring ($t_s = -1.87, n = 230, P = 0.061$) and fall ($t_k = -1.71, n = 180, P = 0.087$). Midge abundance appeared to be a consequence of proximity to the lake, not phenological development.

**DISCUSSION**

We found relatively high numbers of landbirds, including those that breed north of the study area, occurring in nearshore white cedar dominated forests along the northern shore of Lake Huron contrary to our hypothesis about the distribution of spring migrants. There was a similar, although less pronounced effect during fall migration, which was in accordance with our hypothesis about fall migrant distribution. Migrant landbirds concentrated within 0.4 km of the lakeshore during both spring and fall. Landscape features and associated food supply likely contributed to these distributional patterns.

The northern Lake Huron shoreline includes forested islands and peninsulas, coastal wetlands, and different forest types, each of which may influence migrant distribution (Moore et al. 1990, Diehl et al. 2003) or mass gain (Dunn 2000, 2001). We were primarily interested in assessing the influence of northern Lake Huron on migrant abundance and attempted to minimize potentially confounding effects by sampling the predominant forest type, avoiding peninsulas and islands. We also included transect as a factor within our GLM to statistically control for longitudinal and individual transect effects on migrant distribution. Our analysis revealed a significant transect effect for both long- and short-distance migrant distribution in spring and fall, which suggests landscape features other than those associated with the shoreline influence migrant distribution. Our data do not permit us to explore this effect in more detail.

Our results suggest proximity of northern Lake Huron influences migrant distribution even with the influence of uninvestigated landscape features on the spatial distribution of migrants. We found both spring and fall migrants differentially abundant in shoreline habitats. Concentrations of migrating landbirds often occur near large bodies of water including the Gulf of Mexico (Lowery 1945, Gauthreaux 1971, Moore et al. 1990), Great Lakes (Weir 1972, Brock 1992, Bonter et al. 2009), and the Atlantic Coast (Watts and Mahy 1994). The northern Lake Huron shoreline may be attractive to northbound migrants as it is the first landfall for birds flying over Lake Huron and for fall migrants which may accumulate at the shoreline prior to continuing southbound migration. We cannot rule out the lake causes migrants to accumulate in nearshore habitats, but our data suggest other factors, notably presence of midges in nearshore habitats during spring, contributed to migrant distributional differences.

Migrants, including those that breed north of the study area, concentrated at the shoreline even as leaf out was delayed relative to inland areas. A positive correlation between stage of leafout and abundance of leaf-chewing insects in the same area (R. J. Smith and F. R. Moore, unpubl. data) suggests abundance of these insects was lower in shoreline habitats relative to inland areas, especially early in the spring migratory period. Migrant distribution coincided with midge distribution, more migrants were in shoreline habitats during spring and fall, as were midges, and there were positive associations between midge abundance and all three categories of migrant abundance in spring.

The abundance of midges is especially marked in spring, suggesting foraging migrants relied on aquatic-dependent food resources (Smith 2003) disproportionately during spring migration. Spring migrants arrived before many leaves had unfurled (Smith et al. 2007; D. N. Ewert and M. J. Hamas, pers. obs.) during the sampling period and in subsequent years. Most terrestrial invertebrates, except spiders, were also scarce on conifers in shoreline habitat (Smith et al. 2007; P. L. Hudson, pers. comm.). We observed many species in shoreline habitats (e.g., *Empidonax* flycatchers, kinglets, many vireo and warbler species, White-throated Sparrow (*Zonotrichia albicollis*), and White-crowned Sparrow) feeding on midges from foliage, aerially, from rocks along the shoreline, and from spider webs during our spring surveys (Dallman and Smith 1995). Our results, in conjunction with those of Seeffel (1997) and Smith et al. (1998, 2004, 2007), suggest midges are a critical early season resource for spring migrant landbirds moving through nearshore habitats adjacent to northern Lake Huron.

Fall migrants were more abundant in shoreline habitats, as would be predicted if the moderating effect of the lake on nearshore habitats resulted in increased resource abundance relative to inland
habitats. However, fall migrants were more evenly distributed with respect to distance from the shoreline than spring migrants, perhaps because of both a relative absence of midges and abundance of widely distributed phytophagous insects during the peak migration period of late August and early September. Midges were significantly less abundant within shoreline habitats in fall compared to spring, resulting in a reduced shoreline/land contrast in midge abundance. Seefelt (1997) noted migrants feeding on Lepidoptera larvae and adults, Coleoptera, Homoptera, and other taxa both at the shoreline and inland during fall migration, when leaves appear to support a diverse arthropod fauna. Our results suggest midges do not have a prominent role in attracting inland migrants during fall migration, when leaves appear to support a diverse arthropod fauna. Our results suggest midges do not have a prominent role in attracting inland tourists in fall compared to spring, resulting in a reduced shoreline/land contrast in midge abundance.

Seefelt (1997) noted migrants feeding on Lepidoptera larvae and adults, Coleoptera, Homoptera, and other taxa both at the shoreline and inland during fall migration, when leaves appear to support a diverse arthropod fauna. Our results suggest midges do not have a prominent role in attracting fall migrants or those at more northern latitudes, such as central Illinois where migrants fed primarily on geometrid caterpillars (Graber and Graber 1983). The importance of shoreline habitats to migrants may also be affected by timing of midge or other arthropod emergence related to weather or climate changes that modify synchrony between prey abundance and timing of migration (Strode 2003).

Identifying attributes of important stopover sites and then ranking stopover sites for conservation purposes is challenging (Hutto 2000) but in progress (Stralberg et al. 2011). Coastal areas, including the Great Lakes, may be important areas for conservation efforts (Petit 2000) given the high concentrations of birds found along many shorelines and increasing development pressures that threaten these areas (Simons et al. 2000). Identifying and protecting sites where birds can safely and rapidly replenish resources may be critical to maximizing their survival and reproductive success (Moore et al. 1995). Protection of vegetated shorelines, especially those bordered by productive nearshore aquatic communities should benefit migrants both in the Great Lakes region and perhaps elsewhere, including sites at comparable latitudes in the northern USA and Canada. Similar ecological relationships at wetlands (e.g., Sealy 1988), streams (Wilson 2001), and inland lakes may also support many migrants and be disproportionately important to migrant landbirds.

ACKNOWLEDGMENTS

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APPENDIX. Mean number of birds detected per point for each species stratified by distance from the northern Lake
Spring
Distance from shoreline (km)
Ruffed Grouse (Bonasa umbellus)
Sharp-shinned Hawk (Accipiter striatus)

Fall

0.0

0.4

0.8

1.6

0.02

0.02

0.00

3.2

0.0

0.04

Red-shouldered Hawk (Buteo lineatus)

0.00

0.00

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0.00

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0.00

Broad-winged Hawk IB. platypterus)

0.00

0.00

0.00

0.01

0.03

0.01
0.00
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0.00

Mourning Dove (Zenaida macroura)

0.00

0.00

0.00

0.00

Ruby-throated Hummingbird (Arrhilnchu\ cotubris)

0.00

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Belled Kingfisher (Megaceryle alcyon)

0.00

0.00

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Yellow-bellied Sapsucker (Sphyrapicus varius)
Downy Woodpecker (Picoides pubescens)
Hairy Woodpecker {P. vilhsus)
Northern Flicker (Cotuples aural us)

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Yellow-bellied Flycatcher {Empidonax flaviventris)
Unknown Empidonax

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Eastern Kingbird (Tyrannus tyrannus)

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0.00

Black-capped Chickadee <Poecile alricapillus)
Red-breasted Nuthatch (Sitta canadensis)
White-breasted Nuthatch (S. carolincnsis)
Brown Creeper (Certhia americana)
Winter Wren (Troglodytes hi emails )
Golden-crowned Kinglet (Ren ulus sal rape)
Ruby-crowned Kinglet (R. calendula)
Veery (Catharus fuscescens)
Gray-cheeked Thrush (C. minimus)
Swainson's Thrush (C. ustulatus)
Hermit Thrush (C‘. guttatus)
Wood Thrush (Hylocichla mustelina)
American Robin (Turdus migrutorius)
Gray Catbird (DumeteUa carolinensis)
Brown Thrasher (Toxastoma rufum)
Cedar Waxwing (Bombycilia ccdrorum>
Tennessee Warbler (Oreothlypis peregrina)
Nashville Warbler (O. ruficupilla)
Northern Parula (Porula americana)
Yellow Warbler (Dendroica petechia)
Chestnut-sided Warbler (O. pensyhanica)
Magnolia Warbler (D. magnolia)
Cape May Warbler (D. tigrina)
Black-throated Blue Warbler (D. caerulescens)
Yellow-rumped Warbler (D. coronata)
Black-throated Green Warbler (IX virens)
Blackburnian Warbler (D. fused)
Pine Warbler (D. pin,is)
Palm Warbler (D. palmarum)
Bay-breasted Warbler (IX castaneni

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Great Crested Flycatcher (Myiarchus crinitus)

American Crow (Con'us braehyrhynchos)

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Tree Swallow (Tachycincta bicolor)

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Blue Jay (Cyanocitta eristata)

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Red-eyed Vireo (V. olivuceus)

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Philadelphia Vireo (V. philadelphicus)

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Eastern Wood-Pewec (Coni opus vlrens)

Blue-headed Virco (Vireo sotitarius)

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Pileated Woodpecker (Dryocopus pileatus)

Eastern Phoebe (Sayomis phoebe)

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### APPENDIX. Continued.

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<tr>
<td>Black-and-white Warbler (M. varia)</td>
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<td>0.17</td>
<td>0.16</td>
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<tr>
<td>American Redstart (S. ruticilla)</td>
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<td>0.23</td>
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<td>0.14</td>
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STABLE ISOTOPE ANALYSIS OF FALL MIGRATION STOPOVER BY SIX PASSERINE SPECIES IN AN INLAND PITCH PINE-SCRUB OAK BARREN

JEREMY J. KIRCHMAN,1,4 JOEL RALSTON,1,2 AND NEIL A. GIFFORD3

ABSTRACT.—We conducted mist-net surveys of migrating songbirds during fall migration 2007–2009 on the 1,300-ha Albany Pine Bush Preserve (APBP), a fire-managed inland pitch pine–scrub oak (Pinus rigida–Quercus spp.) barren in east-central New York. We banded 244 migrating passerines from 32 non-resident species in 8,610 net/hr documenting use of northeastern pine barrens as stopover sites for passerines with diverse breeding ecologies. We estimated the breeding site origin of six species (a kinglet, four warblers, and a sparrow) using stable hydrogen isotope measurements from flight feathers. There was a broad range of isotope ratios within each species indicating a large catchment area extending several hundred kilometers north and west of the stopover site. Over half the birds originated >750 km from the APBP. We found no evidence for geographical structure of the timing of migration through APBP; slopes of regression lines for capture date versus hydrogen isotope ratio from feathers (δD) were not statistically different from zero. This contrasts with previous isotope research that reports both leapfrog and chain migration patterns by different warbler species at stopover sites in the western United States.

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Pine (Pinus spp.) barrens are globally rare, pyrogenic, early-successional ecosystems that support unique assemblages of species including many rare and declining taxa (Finton 1998, Barnes 2003, Latham 2003, Wagner et al. 2003). Pine barrens in the northeastern United States are dry, nutrient-poor systems restricted to glacial outwash plains and ridges with shallow soils (Barnes 2003). Historically, these habitats were inhospitable to agriculture and remained undeveloped, but extensive suburbanization and suppression of wildfires have reduced the region’s pine barrens and other early-successional habitats >50% since the 1960s (Trani et al. 2001). There are <20 significant pine barrens remaining in the northeastern U.S., including three large, mostly contiguous coastal barrens and several smaller inland pine barrens (Fig. 1). Pine barrens transition to close-canopy forest in the absence of recurring fire (Finton 1998), but extant barrens appear to have persisted since glacial retreat 12,000–18,000 years ago (Barnes 2003) making them uniquely stable habitat for early-successional wildlife species.

Early-successional habitats in northeastern U.S. pine barrens are maintained almost exclusively through active management (Trani et al. 2001). The important targets of these efforts include shrubland birds, the most conservation-reliant (sensu Scott et al. 2010) avian group in the region (Hunter et al. 2001, Detmers 2003). Several studies have documented a 40+ year decline of shrubland and disturbance-dependent bird species (Brawn et al. 2001, Detmers 2003), yet few published studies have described species–habitat relationships for birds breeding in northeastern pine barrens (Kerlinger and Doremus 1981a, b; Morimoto and Wasserman 1991; Grand et al. 2004; Beachy and Robinson 2008; Gifford et al. 2010). We know of no study that has documented the use of pine barrens as migratory stopover sites.

It is now well-recognized that events throughout the annual cycle are critical to survival of bird populations including factors in breeding and wintering areas, as well as at migratory stopover sites (Webster and Marra 2005). Migratory stopover sites are critical diurnal foraging areas for nearly all nocturnal migrants. Foraging resources and predation pressures differ among stopover habitats with important fitness consequences for migrants (Moore et al. 1993). Migrants select among alternative habitats and use stopover sites that maximize foraging efficiency (Moore and Aborn 2000). Most research on stopover sites has focused on woodland or riparian habitats (Winker et al. 1992, Wang et al. 1998), but some studies indicate that shrubland and forest interior breeding species rely disproportionately on early successional habitats during autumn migration (Rode- wald and Brittingham 2004). Migratory connectivity of breeding and stopover sites has demographic, evolutionary, and conservation consequences.
Stable isotope ratios from feathers of migrating individuals that molt prior to autumn migration can be used to examine their approximate breeding latitude (Hobson 2002). These data can be used to estimate the catchment area of stopover sites (Mazerolle et al. 2005), and to connect populations passing through migration monitoring stations to breeding populations.

Our objectives were to: (1) describe the temporal dynamics and species composition of the autumn migratory avifauna of the Albany Pine Bush Preserve (APBP), an inland pine barren in east-central New York, and (2) use stable hydrogen isotope measurements from feathers of captured birds to identify the breeding areas of selected migrant species using the APBP.

METHODS

Study Site.—The 1,300-ha Albany Pine Bush Preserve is southwest of the confluence of the Mohawk and Hudson rivers in east-central New York State, USA (42° 42’ N, 73° 52’ W) at an elevation of 79-110 m (Fig. 1). The Preserve supports at least 14 recognized terrestrial community types (Reschke 1990) but is dominated by a pitch pine (Pinus rigida)–scrub oak (Quercus ilicifolia, Q. prinoides) community (Schneider et al. 1991) with pitch pines in the overstory and scrub oaks and other shrubs (primarily Ericaceae) in the understory. Vegetation communities are
underlain by an extensive glacial outwash plain and a system of parabolic sand dunes (30 m max height) that is uniquely large and extensive compared to other northeastern pine barrens (Barnes 2003). Development, soil disturbance, and fire suppression between 1940 and 1990 resulted in an 81% change of land cover with 40% attributed to permanent habitat removal and 41% resulting from changes in plant community composition and structure (Finton 1998). Nearly half of the plant community change that occurred during this period (18% of total land cover) was replacement of pitch pine-scrub oak barrens and thickets with a closed-canopy deciduous forest, dominated by non-native, highly invasive black locust (Robinia pseudoacacia) (Finton 1998). The APBP is physically fragmented by a network of interstate and local highways, which create distinct blocks of protected lands adjacent to commercial, residential, and agricultural land uses. Ecosystem management, including prescribed fire, mowing, invasive plant removal, and restoration planting has been applied to >500 ha of the Preserve since 1991. The portion of the Preserve where we conducted our survey has supported a mosaic of open- and closed-canopy pitch pine-scrub oak communities since before 1928 (Finton 1998). The survey area contains the largest remaining block (56 ha) of pitch pine-scrub oak barrens in the APBP, encompassing several management units dominated by an open-canopy pitch pine overstory and a relatively dense mosaic of scrub oak and ericaceous shrubs in the understory. Sections of the sampled area experienced wild or prescribed fire in 1981, 1994, 1995, 1999, and 2005.

Mist Netting.—We deployed 6–8 mist nets (6–12 m long, 32–36 mm mesh) along a 0.5-km transect during fall migration 2007, 2008, and 2009. We began our survey in late August 2007 and continued until early November to insure that we sampled the full extent of the migratory period. We focused on the 6-week period from early-September to mid-October in subsequent years. Nets were placed on dune ridges perpendicular to the established foot path through the Preserve. Nets were opened at dawn (0530 hrs in early weeks, 0630 hrs in late weeks) and operated until 1030 hrs, 2–4 days per week. Nets were checked every half-hour and birds were removed to cloth bags for processing. Individuals of resident, non-migratory species (e.g., Downy Woodpecker [Picoides pubescens], Black-capped Chickadee [Poecile atricapillus], Blue Jay [Cyanocitta cristata]), and of migratory species known to breed on the Preserve (e.g., Gray Catbird [Dumetella carolinensis], Eastern Bluebird [Sialia sialis]) were immediately released. Captured migrants were marked with a single aluminum USGS leg band, sampled for a single flight feather, measured, weighed, and released. We classified the age and sex of each bird when possible, but did not attempt to characterize the demographics of the fall migrant avifauna.

Stable Isotope Analysis.—We pulled a single flight feather (remex or rectrix) from each migrant and placed the feather in separate paper envelopes. We selected six species following our initial field season on which to conduct hydrogen isotope analysis on the basis of sample size (>5 individuals captured) and because they are known to completely molt all flight feathers on breeding areas prior to migration. These were Ruby-crowned Kinglet (Regulus calendula), Nashville Warbler (Oreothlypis ruficapilla), Magnolia Warbler (Dendroica magnolia), Palm Warbler (D. palmarum), Blackpoll Warbler (D. striata), and Lincoln’s Sparrow (Melospiza lincolnii). Information on molt schedules was obtained from individual Birds of North America species accounts (Ammon 1995, Williams 1996, Wilson 1996, Hunt and Eliason 1999, Swanson et al. 2008, Dunn and Hall 2010). These species have broad breeding ranges well north of our study site, extending across the boreal forest zone of the U.S. and Canada west to the Canadian Rockies (Nashville Warbler, Palm Warbler) or to Alaska (all other species). Two species (Magnolia Warbler, Nashville Warbler) have breeding ranges that extend into the temperate forest zone south of the study site.

We washed each feather to remove dirt and oils, first with a 0.1% Tween-20 detergent solution followed by two rinses in purified water. This was followed by two rounds of washing in a 2:1 chloroform:methanol solvent solution, each followed by rinsing in purified water. Cleaned feathers were placed in new paper envelopes and mailed to Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University (Flagstaff) for weighing, encapsulation in tin, and hydrogen isotope-ratio mass spectrometry. The CPSIL uses a DELTA plus XL Thermo Electron gas isotope-ratio mass spectrometer to measure the hydrogen isotope ratio (δD) from each feather sample. Machines and procedures are calibrated...
so results are comparable to $\delta D_f$ measured in other major research laboratories. Feathers were handled only with fine forceps during washing and subsequent processing.

A series of t-tests performed within each species indicated no significant differences in hydrogen isotope values from feathers collected in different years, and we pooled data from all 3 years in subsequent analyses. We regressed $\delta D_t$ on capture date to examine possible trends with respect to timing of stopover of birds from different breeding localities. We converted $\delta D_p$ to altitude-corrected growing-season precipitation values ($\delta D_p$) using the equation $\delta D_p = \delta D - 25\%$ (Mazerolle et al. 2005) and compared these to the growing season $\delta D_p$ map for North America constructed by Meehan et al. (2004). We used ArcGIS (9.3.1) to overly the $\delta D_p$ map with digital maps of the breeding ranges for each species taken from Ridgely et al. (2007; downloaded from http://www.natureserve.org/getData/birdMaps.jsp). Area of origin maps were produced by highlighting the intersection of the breeding range with the observed range of $\delta D_p$ values we calculated for each species.

**RESULTS**

We banded 244 migratory birds from 32 species in 8,610 net/m/hrs over 3 years (Fig. 2). Both number of migrants captured per unit effort and species diversity peaked in mid- to late-September, weeks 2 and 3 of our 6-week survey period (Fig. 2). Most species pass through the APBP in 2 or 3 weeks, but Nashville Warbler and Yellow-rumped Warbler (*Dendroica coronata*) are present over the course of 5 weeks. No species was captured in both the first and last week of the survey period. The fall migration begins with a trickle of warblers, quickly builds to a diverse assemblage of songbirds from several passeriform families, and ends with a large influx of cold-tolerant species, mostly sparrows that breed at very high latitudes and altitudes.

Stable hydrogen isotope values from feathers ($\delta D_h$) of six species ranged widely, indicating the birds came from breeding sites across the boreal forest (Table 1). Mapped $\delta D_p$ calculated from $\delta D_t$ measurements overlapped with known breeding ranges of all species. Slopes of regressions between date of capture and $\delta D_t$ were not statistically different from zero for all species ($all$ $r^2 < 0.05$, all $P > 0.05$). We found no correlations to indicate that individuals from more southerly breeding areas arrived earlier (chain migration) or that more

![FIG. 2. Autumn migrants captured on the Albany Pine Bush Preserve during 6-week mist-net surveys in 2007, 2008, and 2009. Totals are for all 3 years combined.](image-url)

<table>
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<th>Species</th>
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<tr>
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<td>Blackpoll Warbler</td>
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<td>Lincoln’s Sparrow</td>
<td>-129.52 to -77.85</td>
<td>-97.34 (7)</td>
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northerly birds arrived earlier (leap-frog migration) (Fig. 3).

The generally east-to-west inclination of the isotope contours from the growing season model for North America precludes precise delineation of the longitude of the breeding sites of captured migrants. Our data indicate that 32 of 61 individuals from all six species had $\delta D_f$ values $<-100\%$, corresponding to the $-75\%$ $\delta D_p$ contour, which is at least 750 km north of the APBP (Fig. 4). Only for Palm Warbler (6 of 19 individuals) and Lincoln’s Sparrow (2 of 7 individuals) did $<50\%$ of individuals originate southeast of the $-75\%$ $\delta D_p$ contour. Blackpoll Warblers had $\delta D_f$ values of -170.86 to -123.85 (mean of 8 measurements = -148.64), indicating breeding sites that are at least 1,500 km north or northwest of APBP (Fig. 4). These patterns are noteworthy because all six species selected have breeding populations in New York’s Adirondack Mountains ~100 km north of the APBP. It is possible that some Ruby-crowned Kinglets, Nashville Warblers, and Magnolia Warblers originated in the Adirondacks, but most individuals of even these species come from much farther north.

DISCUSSION

Our data indicate early successional habitat maintained by fire on inland pine barrens attracts migrating species that do not breed in these habitats. A number of the captured species breed in early successional shrubland habitats (e.g., Tennessee Warbler [$Oreothlypis peregrina$], Nashville Warbler), but most species captured breed exclusively in closed-canopy deciduous forests and spruce-fir ($Picea-Abies$) dominated boreal forests. We did not attempt to quantify the importance of pine barrens as stopover sites relative to other habitat types, but comparison of our capture data (Fig. 2) to those obtained over the same time period (Fall 2007–2009) at the well-studied Braddock Bay Bird Observatory (BBBO) indicates all species captured at APBP were also present at BBBO. The Braddock Bay site, on the southern shore of Lake Ontario near Rochester, New York, ~300 km WN W of the APBP, supports a mosaic of abandoned fields, early-successional landcover, and second-growth forest (Bonter et al. 2007). A large staff of scientists and volunteers at BBBO operate 20–30 mist nets every day during the fall migration, resulting in a much greater effort.

[Graph of stable hydrogen isotope values measured from feathers ($\delta D$) of six species captured in the Albany Pine Bush Preserve and date of capture. Slopes of regression lines (not shown) are not statistically different from zero (Ruby-crowned Kinglet $r^2 = 0.0487$, $P = 0.67$, $n = 6$; Nashville Warbler $r^2 = 0.0084$, $P = 0.75$, $n = 13$; Palm Warbler $r^2 = 0.0007$, $P = 0.91$, $n = 19$; Blackpoll Warbler $r^2 = 0.0192$, $P = 0.74$, $n = 8$; Magnolia Warbler $r^2 = 0.0096$, $P = 0.81$, $n = 8$; Lincoln’s Sparrow $r^2 = 0.0367$, $P = 0.68$, $n = 7$).]
Fig. 4. Breeding range catchment areas for six passerine species captured in the Albany Pine Bush Preserve. Gray shading indicates the gradient of stable hydrogen isotope values in growing season precipitation ($\delta^{18}O$) at 15‰ contours. Hatching indicates the overlap of the range of $\delta^{18}O$ values obtained from feathers with the breeding range of each species. The star indicates the locality of APBP.
Our hydrogen isotope analysis of the timing of stopover at the APBP with respect to latitude of breeding origin failed to reveal any correlation between stopover date and breeding latitude for our six target species (Fig. 3). Previous research (Kelly et al. 2002, Kelly 2006) has shown both negative and positive correlations for different fall migrating warbler species that stopover at the Bosque del Apache National Wildlife Refuge in New Mexico, some species (Orange-crowned Warbler (Oreothlypis celata), Common Yellowthroat (Geothlypis trichas)) breeding at southern latitudes arrived earlier than birds breeding at northern latitudes, whereas for other species (Yellow Warbler (Dendroica petechia), Wilson’s Warbler) the reverse was true. Our failure to find any trends by our six study species may be due to our small sample size, although Kelly et al. (2002) had similar sample sizes of Common Yellowthroat (n = 19), Orange-crowned warbler (n = 17), and Yellow Warbler (n = 18). Ours is the first attempt to use the hydrogen isotope approach to characterize the chronology of migration within species in eastern North America, and our results indicate migration through eastern North America is less geographically structured than in the western U.S. Several other fundamental differences exist between the eastern and western songbird migration systems (Kelly and Hutto 2005) including taxonomic composition, relative use of fat metabolism, diet, and habitat use. Movement patterns are also apparently highly variable among passerine species (Kelly et al. 2002, Kelly 2006), and fall migration may be geographically structured in other species that pass through our study site. The isotope data indicate catchment areas for all six study species were large and extended to regions of the boreal forest hundreds of kilometers from our study site (Fig. 4). This finding is similar to previously reported catchment areas estimated for other species of passerines at migration monitoring stations in Manitoba (Wassenaar and Hobson 2001, Mazzerolle et al. 2005) and southern Ontario (Wassenaar and Hobson 2001). Thus, catchment areas of migratory stopover sites vary considerably among species. The estimated catchment areas of five of our six study species included regions north of the APBP, and extending well to the east and west (Fig. 4). The isotope approach does not allow distinguishing among all potential source areas within a given 8D2 contour. Thus, it is not possible to identify how far east or west the birds that stopover on the APBP may originate. Most passerine species migrate in a generally north-south direction that parallels mountain ranges, major river valleys, and coastlines. We suspect the catchment areas we mapped overestimate the western extent of true catchment areas, and populations originating near the western edge of our catchment areas are not passing through APBP. An exception may be the Blackpoll Warbler, which has a unique transoceanic migratory pathway (Nisbet et al. 1995, Hunt and Elison 2001). Individual Blackpoll Warblers migrate in a general eastward direction, collecting along the Atlantic Coast in Maritime Provinces and the northeastern United States. Blackpoll Warblers then migrate over the Atlantic Ocean to wintering areas in northern South America. Our data support the hypothesis that individuals breeding just north and east of the APBP in New York, New England, Ontario, and the Maritime Provinces do not pass through APBP as they migrate east. Our hydrogen isotope analysis of six species
that pass through the APBP adds taxonomic and geographic breadth to research on the timing of songbird migration and quadruples the number of species for which catchment areas have been estimated with this method. Wassenaar and Hobson (2001) found the catchment area for Swainson's Thrushes ( Catharus ustulatus) was much larger at Long Point, Ontario, than at Delta Marsh in Manitoba, suggesting that sites further along a migratory pathway will have larger catchment areas. The APBP may draw migrants from a larger area because it is southeast of those stopover sites. Comparisons among sites and among species may result in new insights regarding migratory pathways and the importance of specific stopover habitats as more hydrogen isotope data are published.

ACKNOWLEDGMENTS

We thank staff members of the Albany Pine Bush Preserve Commission (APBPC), the New York State Department of Environmental Conservation (NYSDEC), and the New York State Office of Parks, Recreation and Historic Places (OPRHP) for assistance with field work, especially Tray Bisaldi and Laura Bried. We thank Brad Stratton for making the maps in Figures 1 and 4. Funding for isotope laboratory work was provided by NYSDEC and APBPC. Annata Moghe assisted with processing of feather samples. Funding and logistical support for field work was provided by the New York State Museum, a division of the New York State Education Department, and by the New York State Bird Conservation Areas program administered by the OPRHP and the NYSDEC. We thank C. E. Brown, Jason Bried, Kathy Schneider, and two anonymous reviewers for helpful comments on this paper.

LITERATURE CITED


LONG-TERM SHIFTS IN AUTUMN MIGRATION BY SONGBIRDS AT A COASTAL EASTERN NORTH AMERICAN STOPOVER SITE

SUSAN B. SMITH1,2,3 AND PETER W. C. PATON1

ABSTRACT.—We investigated long-term trends in mean autumn capture dates of 19 species of migratory passerines including 11 long-distance migrants and eight short-distance migrants. Birds were captured between 1960 and 2007 at a banding station in southern Rhode Island. We detected annual trends in the highest ranked models with mean capture dates of seven species significantly delayed by an average of 3.0 days per decade; 38% of long-distance migrants and 50% of short-distance migrants studied significantly delayed migration. We found no evidence of long-term shifts in autumn migration timing for seven species and mean capture dates of five species exhibited non-linear annual trends. Mean autumn temperature was an important factor in explaining annual trends for eight species. Changes in annual capture rates for some species may have an equal or greater role than year or temperature in explaining long-term trends in autumn migration timing. Our analysis suggests that some migratory bird species are now departing the region later than in the 1960s. Important differences among species and regions are likely to influence species-specific responses to changes in climate patterns. Received 30 August 2010. Accepted 9 February 2011.

The rise in global temperatures in recent decades has affected the phenology of many biological events across a variety of organisms and trophic levels (Walther et al. 2002, Parmesan and Yohe 2003, Visser and Both 2005). Avian migration may be particularly sensitive to climate change because many species rely on environmental stimuli, in addition to intrinsic cues, to initiate major events during their annual cycle. There is growing evidence that many European passerines are responding to annual fluctuations in local air temperatures and large-scale climatic perturbations by shifting the timing of annual migrations (Lehikoinen et al. 2004, Gienapp et al. 2007, Gordo 2007, Rubolini et al. 2007). Passerines in North America, where the rate of climate change is not as pronounced as in Europe, exhibit a trend towards earlier spring migration, although not as consistently as in most European studies (Gordo 2007, MacMynowski et al. 2007, Miller-Rushing et al. 2008, Van Buskirk et al. 2009). The ability of birds to adapt to climate change by adjusting timing of spring migration has clear consequences for breeding success because mis-timing of breeding events with peak food resources has been linked to population declines (Both et al. 2006, Visser et al. 2006, Leech and Crick 2007, Möller et al. 2008).

The potential effects of global warming trends on timing of autumn migration are inherently more complex and fewer studies have examined changes in autumn departure or migration passage dates. European and North America studies of the chronology of passerine migration in autumn have provided mixed results. Some studies reported delays or advances while others have reported an absence of long-term trends (Lehikoinen et al. 2004, Mills 2005, Gordo 2007, MacMynowski and Root 2007, Van Buskirk et al. 2009). In addition, the strength and direction of long-term trends and phenological responses to climate change appear to be variable among species (Jenni and Kéry 2003, Tøttrup et al. 2006, Thorup et al. 2007).

We analyzed annual variation in the mean autumn passage dates of 19 passerine species during stopover in southern Rhode Island using 45 years of data from the Kingston Wildlife Research Station, one of the longest operational migration monitoring stations in eastern North America. Our objectives were to: (1) examine whether mean passage dates of migrating passerines are changing over time, (2) assess if variation in migration chronology could be explained by annual changes in local autumn temperatures, and (3) consider the influence of annual capture rates on our interpretations because fluctuations in population sizes may influence estimates of annual migration timing (Miller-Rushing et al. 2008).

METHODS

Study Site.—We conducted field work at the Kingston Wildlife Research Station (KWRS) in South Kingstown, Rhode Island, USA (41° 27’ N,
We used an information-theoretic approach to examine if linear, quadratic, and cubic functions best described these relationships for a given species. We calculated second-order Akaike's Information Criterion (AIC) and used Akaike weights (w) to rank models (Burnham and Anderson 2002). Our objective was to assess patterns over time and we were not using these models for prediction, but we accepted the model with the highest Akaike weight as the best model. AICc, model selection results indicated that...
TABLE 1. Model selection results for the highest ranked candidate AICr models that explain mean capture rate of 11 long-distance migrants captured at Kingston Wildlife Research Station, Rhode Island, between 1960 and 2007. Models are ranked based on Akaike weights (w) and only models with Δ, < 2.0 are shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>n</th>
<th>RSS</th>
<th>Maximized log(L)^a</th>
<th>AICr</th>
<th>Δ</th>
<th>w</th>
<th>w/(w^*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Redstart (Setophaga ruticilla)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>44 (1,598)</td>
<td>772.02</td>
<td>-63.03</td>
<td>132.65</td>
<td>0.0</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>44 (1,598)</td>
<td>762.39</td>
<td>-62.75</td>
<td>134.53</td>
<td>1.9</td>
<td>0.17</td>
<td>2.5</td>
</tr>
<tr>
<td>Y = temp + caprate</td>
<td>4</td>
<td>44 (1,598)</td>
<td>763.42</td>
<td>-62.78</td>
<td>134.58</td>
<td>1.9</td>
<td>0.17</td>
<td>2.6</td>
</tr>
<tr>
<td>Black-and-white Warbler (Mniotilta varia)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>39 (652)</td>
<td>1,073.48</td>
<td>-64.64</td>
<td>135.97</td>
<td>0.0</td>
<td>0.43</td>
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<td>39 (652)</td>
<td>1,036.29</td>
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<td>137.09</td>
<td>1.1</td>
<td>0.25</td>
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<td>4</td>
<td>39 (652)</td>
<td>1,041.32</td>
<td>-64.05</td>
<td>137.28</td>
<td>1.3</td>
<td>0.22</td>
<td>1.9</td>
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<tr>
<td>Blackpoll Warbler (Dendroica striata)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>26 (386)</td>
<td>616.69</td>
<td>-41.16</td>
<td>92.23</td>
<td>0.0</td>
<td>0.56</td>
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<tr>
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<td>3</td>
<td>26 (386)</td>
<td>733.51</td>
<td>-43.42</td>
<td>93.92</td>
<td>1.7</td>
<td>0.24</td>
<td>2.3</td>
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<tr>
<td>Blue-winged Warbler (Vermivora cyanoptera)</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>42 (838)</td>
<td>1,126.24</td>
<td>-69.07</td>
<td>144.77</td>
<td>0.0</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>42 (838)</td>
<td>1,153.45</td>
<td>-69.57</td>
<td>145.77</td>
<td>1.0</td>
<td>0.17</td>
<td>1.7</td>
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<tr>
<td>Y = caprate</td>
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<td>1,155.66</td>
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<td>145.85</td>
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<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>42 (838)</td>
<td>1,095.65</td>
<td>-68.49</td>
<td>146.06</td>
<td>1.3</td>
<td>0.15</td>
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<td>4</td>
<td>42 (838)</td>
<td>1,098.56</td>
<td>-68.55</td>
<td>146.17</td>
<td>1.4</td>
<td>0.14</td>
<td>2.0</td>
</tr>
<tr>
<td>Common Yellowthroat (Geothlypis trichas)</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + year^2</td>
<td>4</td>
<td>44 (1,943)</td>
<td>698.12</td>
<td>-60.81</td>
<td>130.65</td>
<td>0.0</td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td>Y = year + year^2 + caprate</td>
<td>5</td>
<td>44 (1,943)</td>
<td>685.58</td>
<td>-60.41</td>
<td>132.41</td>
<td>1.8</td>
<td>0.21</td>
<td>2.4</td>
</tr>
<tr>
<td>Gray Catbird (Dumetella carolinensis)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + year^2 + year^2 + caprate</td>
<td>6</td>
<td>45 (4,840)</td>
<td>650.55</td>
<td>-60.10</td>
<td>134.41</td>
<td>0.0</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>Y = year + year^3 + year^2</td>
<td>5</td>
<td>45 (4,840)</td>
<td>692.74</td>
<td>-61.51</td>
<td>134.57</td>
<td>0.2</td>
<td>0.37</td>
<td>1.1</td>
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<tr>
<td>Northern Waterthrush (Parkesia noveboracensis)</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + caprate</td>
<td>4</td>
<td>23 (197)</td>
<td>749.18</td>
<td>-40.06</td>
<td>90.34</td>
<td>0.0</td>
<td>0.30</td>
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<tr>
<td>Y = year</td>
<td>3</td>
<td>23 (197)</td>
<td>873.32</td>
<td>-41.82</td>
<td>90.91</td>
<td>0.6</td>
<td>0.23</td>
<td>1.3</td>
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<tr>
<td>Y = caprate</td>
<td>3</td>
<td>23 (197)</td>
<td>899.91</td>
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<td>91.60</td>
<td>1.3</td>
<td>0.16</td>
<td>1.9</td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>23 (197)</td>
<td>907.02</td>
<td>-42.26</td>
<td>91.78</td>
<td>1.4</td>
<td>0.15</td>
<td>2.0</td>
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<tr>
<td>Oveiird (Sialia aurocapilla)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = caprate</td>
<td>3</td>
<td>42 (554)</td>
<td>1,479.33</td>
<td>-74.80</td>
<td>156.22</td>
<td>0.0</td>
<td>0.32</td>
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<tr>
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<td>42 (554)</td>
<td>1,521.75</td>
<td>-75.39</td>
<td>157.41</td>
<td>1.2</td>
<td>0.18</td>
<td>1.8</td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>42 (554)</td>
<td>1,521.87</td>
<td>-75.39</td>
<td>157.41</td>
<td>1.2</td>
<td>0.18</td>
<td>1.8</td>
</tr>
<tr>
<td>Y = year + caprate</td>
<td>4</td>
<td>42 (554)</td>
<td>1,458.20</td>
<td>-74.49</td>
<td>158.07</td>
<td>1.8</td>
<td>0.13</td>
<td>2.5</td>
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<tr>
<td>Red-eyed Vireo (Vireo olivaceus)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>32 (385)</td>
<td>2,196.50</td>
<td>-67.66</td>
<td>142.18</td>
<td>0.0</td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>32 (385)</td>
<td>2,104.33</td>
<td>-66.98</td>
<td>143.43</td>
<td>1.3</td>
<td>0.26</td>
<td>1.9</td>
</tr>
<tr>
<td>Veery (Catharus fuscescens)</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>38 (505)</td>
<td>827.68</td>
<td>-58.54</td>
<td>123.79</td>
<td>0.0</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>38 (505)</td>
<td>854.18</td>
<td>-59.14</td>
<td>124.98</td>
<td>1.2</td>
<td>0.22</td>
<td>1.8</td>
</tr>
<tr>
<td>Wood Thrush (Hylocichla mustelina)</td>
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<td></td>
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<td></td>
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</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>35 (400)</td>
<td>1,024.11</td>
<td>-59.08</td>
<td>124.94</td>
<td>0.0</td>
<td>0.30</td>
<td></td>
</tr>
<tr>
<td>Y = caprate</td>
<td>3</td>
<td>35 (400)</td>
<td>1,049.98</td>
<td>-59.52</td>
<td>125.82</td>
<td>0.9</td>
<td>0.19</td>
<td>1.6</td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>35 (400)</td>
<td>1,050.88</td>
<td>-59.54</td>
<td>125.85</td>
<td>0.9</td>
<td>0.19</td>
<td>1.6</td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>35 (400)</td>
<td>1,003.50</td>
<td>-58.73</td>
<td>126.79</td>
<td>1.8</td>
<td>0.12</td>
<td>2.6</td>
</tr>
</tbody>
</table>

a Parameters: Y = mean capture date, temp = mean maximum daily temperature between 7 August and 31 October, and caprate = annual capture rate calculated as the number of birds captured per 100 net hrs between 7 August and 31 October.

b Number of estimable regression parameters: k = model order = number of predictors + 1.

c Number of years included in analyses. Total number of birds captured in all years included between 1960 and 2007 is in parentheses.
d Calculated as (-6*Se[log,RSS/df]) where RSS is the residual sum of squares.

* Evidence ratio where w = the highest ranked model.
TABLE 2. Model selection results for the highest ranked candidate AICc models that explain mean capture date of eight short-distance migrants at Kingston Wildlife Research Station, Rhode Island, between 1960 and 2007. Models are ranked based on Akaike weights (w_i) and only models with Δ_i < 2.0 are shown.

<table>
<thead>
<tr>
<th>Model*</th>
<th>K*</th>
<th>n</th>
<th>RSS</th>
<th>Maximized log(L/L0)</th>
<th>AICc</th>
<th>Δ</th>
<th>w_i</th>
<th>w_i/a_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern Towhee (Pipilo erythrophthalmus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>39 (714)</td>
<td>3,830.83</td>
<td>-89.45</td>
<td>185.59</td>
<td>0.0</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
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<td>39 (714)</td>
<td>3,743.66</td>
<td>-89.00</td>
<td>187.18</td>
<td>1.6</td>
<td>0.23</td>
<td>22</td>
</tr>
<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>34 (690)</td>
<td>710.93</td>
<td>-51.68</td>
<td>110.17</td>
<td>0.0</td>
<td>0.35</td>
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</tr>
<tr>
<td>Y = caprate</td>
<td>4</td>
<td>34 (690)</td>
<td>743.87</td>
<td>-52.45</td>
<td>111.71</td>
<td>1.5</td>
<td>0.16</td>
<td>22</td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>34 (690)</td>
<td>744.13</td>
<td>-52.46</td>
<td>111.72</td>
<td>1.6</td>
<td>0.16</td>
<td>22</td>
</tr>
<tr>
<td>Y = year + caprate</td>
<td>4</td>
<td>34 (690)</td>
<td>697.84</td>
<td>-51.37</td>
<td>112.11</td>
<td>1.9</td>
<td>0.13</td>
<td>26</td>
</tr>
<tr>
<td>Hermit Thrush (Catharus guttatus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>40 (680)</td>
<td>398.49</td>
<td>-45.98</td>
<td>101.09</td>
<td>0.0</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td>Ruby-crowned Kinglet (Regulus calendula)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>37 (554)</td>
<td>3,562.43</td>
<td>-83.43</td>
<td>173.58</td>
<td>0.0</td>
<td>0.27</td>
<td></td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>37 (554)</td>
<td>3,424.31</td>
<td>-83.76</td>
<td>174.25</td>
<td>0.7</td>
<td>0.19</td>
<td>1.4</td>
</tr>
<tr>
<td>Y = temp + caprate</td>
<td>4</td>
<td>37 (554)</td>
<td>3,202.23</td>
<td>-82.52</td>
<td>174.30</td>
<td>0.7</td>
<td>0.19</td>
<td>1.4</td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>37 (554)</td>
<td>3,222.47</td>
<td>-82.64</td>
<td>174.53</td>
<td>0.9</td>
<td>0.17</td>
<td>1.6</td>
</tr>
<tr>
<td>Song Sparrow (Melospiza melodia)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year</td>
<td>3</td>
<td>37 (554)</td>
<td>3,424.31</td>
<td>-83.76</td>
<td>174.25</td>
<td>0.7</td>
<td>0.19</td>
<td>1.4</td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>37 (554)</td>
<td>3,202.23</td>
<td>-82.52</td>
<td>174.30</td>
<td>0.7</td>
<td>0.19</td>
<td>1.4</td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>37 (554)</td>
<td>3,222.47</td>
<td>-82.64</td>
<td>174.53</td>
<td>0.9</td>
<td>0.17</td>
<td>1.6</td>
</tr>
<tr>
<td>Swamp Sparrow (M. georgiana)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = temp</td>
<td>3</td>
<td>34 (417)</td>
<td>326.83</td>
<td>-38.47</td>
<td>83.74</td>
<td>0.0</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td>White-throated Sparrow (Zonotrichia albicollis)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + year 2 + temp</td>
<td>5</td>
<td>45 (2.728)</td>
<td>349.64</td>
<td>-46.13</td>
<td>103.80</td>
<td>0.0</td>
<td>0.59</td>
<td></td>
</tr>
<tr>
<td>Yellow-rumped Warbler (Dendroica coronata)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y = year + temp + caprate</td>
<td>5</td>
<td>42 (3,044)</td>
<td>321.83</td>
<td>-42.76</td>
<td>97.19</td>
<td>0.0</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>Y = year + caprate</td>
<td>4</td>
<td>42 (3,044)</td>
<td>355.66</td>
<td>-44.86</td>
<td>98.81</td>
<td>1.6</td>
<td>0.20</td>
<td>2.3</td>
</tr>
<tr>
<td>Y = year + temp</td>
<td>4</td>
<td>42 (3,044)</td>
<td>358.20</td>
<td>-45.01</td>
<td>99.10</td>
<td>1.9</td>
<td>0.18</td>
<td>2.6</td>
</tr>
</tbody>
</table>

* Parameters: Y = mean capture date; Temp = mean maximum daily temperature between 7 August and 31 October; Caprate = annual capture rate calculated as the number of birds captured per 100 net hours between 7 August and 31 October.
* Number of estimatable regression parameters in model including intercept and variance.
* Number of years included in analyses. Total number of birds captured in all years included between 1960 and 2007 is in parentheses.
* Calculated as (0.5n* log10(RSS/n)) where RSS is the residual sum of squares.
* Evidence ratio where w_i = the highest ranked model.

We assessed the relative importance of year (using the model selected in the analysis), mean autumn temperature, and annual capture rates for explaining variation in mean capture date. We used mean arrival dates in our analysis, rather than first arrival dates based on research by Mills (2005) and Miller-Rushing et al. (2008) (see also Van Buskirk et al. 2009). We evaluated a candidate model set for each species that included all combinations of the predictor variables. We calculated AICc and w_i and used differences in AICc (Δ_i = AICc_j - AICc_min) to rank candidate models and considered models with Δ_i < 2 to be substantially supported (Burnham and Anderson 2002). We also calculated evidence ratios (w_i/w_j).

mean autumn temperature and annual capture rate for each species were linearly related to year; thus, we assumed linear relationships between mean autumn temperature or annual capture rate and mean capture date.

We used linear regression to assess the relationship between year and mean autumn temperature (including 1995–1997). We used linear regression to test for long-term trends in mean capture dates over time for species for which a linear function best described the relationship between year and mean capture date in the AIC analyses. We examined residual plots to confirm that data met normality and variance assumptions.
to examine the relative likelihood of each model compared to the highest ranked model, and the relative importance \((w + j)\) of each explanatory variable by summing \(w_j\) across all candidate models in which that variable occurs (Burnham and Anderson 2002). We set a significance level of \(P < 0.05\) for all statistical tests.

**RESULTS**

Mean autumn temperatures in Kingston, Rhode Island increased by 0.03 ± 0.01 °C per year between 1960 and 2007 \((F_{1,46} = 10.4, P < 0.01, \rho^2 = 0.19)\). Year was included in the highest ranked models explaining variation in mean capture dates for seven of 11 long-distance migrants (Table 1) and seven of eight short-distance migrants (Table 2). Models including year only were the highest ranked for four long-distance migrants (Table 1), and four short-distance migrants (Table 2). Models including only mean autumn temperature were the highest ranked for four species: American Redstart \(\text{(Setophaga ruticilla)}\), Blue-winged Warbler \(\text{(Vermivora cyanoptera)}\), Veery \(\text{(Caitharus fuscescens)}\), and Swamp Sparrow \(\text{(Melospiza georgiana)}\) (Tables 1, 2). However, multiple models were also plausible for all species except Hermit Thrush \(\text{(Catharus guttatus)}\), Ruby-crowned Kinglet \(\text{(Regulus calendula)}\), and Swamp Sparrow \(\Delta_1 < 2; \text{Tables 1, 2)}\). These other models included annual capture rate for eight long-distance migrants (Table 1) and four short-distance migrants (Table 2). Annual capture rate alone was the highest ranked model explaining variation in mean capture date for the Ovenbird \(\text{(Seiurus aurocapilla)}\) (Table 1).

Relative importance values revealed that year was the most likely of the three variables to explain variation in mean capture date for 14 species (Table 3). Mean autumn temperature had comparatively high relative importance for one long-distance migrant and three short-distance migrants (Table 3). Annual capture rate was of high relative importance for Yellow-rumped Warbler \(\text{(Dendroica coronata)}\), and followed year closely in terms of relative importance values for Northern Waterthrush \(\text{(Parkesia noveboracensis)}\) (Table 3). There was a significant positive linear trend for mean capture date from 1960 to 2007 for seven of 19 species (Figs. 1, 2) with significant relationships for three of 11 long-distance migrants and four of eight short-distance migrants (Figs. 1, 2). Five species had a nonlinear relation between mean capture date and year (Fig. 3).

Mean autumn temperature had the highest relative importance for two long-distance migrants and two short-distance migrants (Table 3). However, relative importance of mean autumn temperature was similar to that for year for Song Sparrow \(\text{(Melospiza melodia)}\), and distinctions between relative importance values for the three variables were small for Blue-winged Warbler (Table 3). Annual capture rate had the highest relative importance for Ovenbird, and year and mean autumn temperature were similar in relative importance (Table 3).

**DISCUSSION**

We documented significant long-term delays in timing of the migration period for birds at a coastal stopover site in southern New England; 38% of long-distance migrants \((n = 8)\) and 50% of short-
FIG. 1. Relationship between mean Julian capture date and year for eight long-distance migrant species captured at Kingston Wildlife Research Station, Rhode Island, between 1960 and 2007. Trend lines are shown for species with significant linear trends in mean capture date over time.
distance migrants \((n = 6)\) significantly delayed migration based on 45 years of banding records. These species delayed migration chronology by an average of 3.0 days per decade; long-distance migrants delayed migration by an average of 3.3 days per decade, while short-distance migrants delayed migration by 2.8 days per decade. These shifts are similar to those reported by Mills (2005) at Long Point Bird Observatory, Canada, where four short-distance migrants and one long-distance migrant exhibited significant delays averaging 3.0 days per decade. However, Mills (2005) also reported mean advancement of migration by an average of 3.7 days per decade in two long-distance migrants, while we did not detect evidence of any species arriving earlier at the stopover site we monitored. We found no evidence of long-term shifts in migration chronology during autumn for seven of 19 species, which concurs with MacMynowski and Root (2007). These authors found no evidence of timing shifts during autumn migration based on birds killed at a building in Chicago from 1979 to 2002. Van Buskirk et al. (2009) also reported no overall changes in timing of autumn migration over a period of 46 years in western Pennsylvania.

The pattern of delayed migration that we documented agrees with at least one European
Three long-distance migrant species and two short-distance migrant species at Kingston Wildlife Research Station, Rhode Island, which exhibited non-linear relationships between mean capture date and year between 1960 and 2007. Trend lines were generated from the highest ranked model using AIC model selection following polynomial regression analysis.

FIG. 3. Annual trends in mean Julian capture date for three long-distance migrant species and two short-distance migrant species at Kingston Wildlife Research Station, Rhode Island, which exhibited non-linear relationships between mean capture date and year between 1960 and 2007. Trend lines were generated from the highest ranked model using AIC model selection following polynomial regression analysis.

study (Lehikoinen et al. 2004), while other European researchers reported mixed results (Sokolov et al. 1999, Jenni and Kéry 2003, Thorup et al. 2006, Sparks et al. 2007), and some reported overall trends only towards advancing autumn migration (Colton 2003, Thorup et al. 2007). Thus, based on research conducted to date in North America and Europe, there are no consistent patterns in long-term trends in autumn migration of songbirds and the delays reported in our study are likely to be regionally specific.

Explanations for the interspecific variation in autumn migration timing observed in European and North American studies have centered around species-specific traits. These traits include migration distance or number of broods, time and energy required to complete molt prior to migration, and selective pressure for early arrival in wintering areas (Jenni and Kéry 2003, Mills 2005, Thorup et al. 2006, Hedenström et al. 2007). The implications of climate-induced changes in timing of autumn migration are not as closely tied to breeding and reproductive success as shifts in spring migration. However, they may indirectly affect fitness and population stability because shifts in autumn passage dates...
can dictate the composition of species assemblages and number of individuals competing for resources at a given site. This can impact reftueling performance, subsequent arrival and condition in wintering areas and, ultimately, survivorship (Bürlin and Hüppop 2004, Stokke et al. 2005, Gordo 2007).

We documented interdecadal variation in three long-distance migrants (Common Yellowthroat [Geothlypis trichas], Veery, Gray Catbird [Dumetella carolinensis]) and two short-distance migrants (Ruby-crowned Kinglet, White-throated Sparrow [Zonotrichia albicollis]). Other variables not considered in our study could be more important than autumn temperature or annual capture rates for explaining long-term trends in these species. The unusual pattern observed for Gray Catbirds may be because some of the birds we captured are local residents in southern Rhode Island. Thus, opposing shifts among decades may be attributed to population fluctuations, as indicated by the relative importance of annual capture rate for explaining additional variation in mean capture dates in catbirds.

Several species in our study (7 of 19) exhibited no significant long-term shifts in autumn migration timing. For these species, it is difficult to disentangle whether birds are unable to adjust the timing of their migration (e.g., they rely heavily on endogenous cues unrelated to environmental variables), or whether shifts in migration timing were masked by other sources of variation that influence mean passage dates (Törnup et al. 2006, Van Buskirk et al. 2009). Fluctuations in annual capture rates explained little variation in mean capture date and are unlikely to have influenced most species in our study (Miller-Rushing et al. 2008). However, changes in annual capture rates or population sizes for two species, Ovenbird and Northern Waterthrush, may in part explain the absence of long-term shifts in autumn timing.

The influence of rising global temperatures on timing of autumn migration in North American passerines may be difficult to predict given the observed variation in the strength of response among species in different regions. The availability of long-term data sets limits analyses of phenological shifts to long-term banding operations or study sites. However, more study is needed across a broader geographic scale, particularly in coastal regions, and at different points on the migration route to accurately assess conservation implications and develop management strategies that address the impacts of phenological shifts in autumn migration.

ACKNOWLEDGMENTS

We are greatly indebted to D. L. Kraus for his generosity and commitment to the study of migratory birds. We thank the Audubon Society of Rhode Island for property maintenance and housing at the Kingston Wildlife Research Station. We also thank S. R. McWilliams, J. E. Osenkowski, B. J. Pierce, and Lynn Duda for assisting with the banding operation and creating the electronic banding data base.

LITERATURE CITED


HABITAT USE OF THE LOUISIANA WATERTHRUSH DURING THE NON-BREEDING SEASON IN PUERTO RICO

MICHAEL T. HALLWORTH,1,3 LEONARD R. REITSMA,1 AND KYLE PARENT1

ABSTRACT.—We used radiotelemetry to quantify habitat and spatial use patterns of neighboring Louisiana Waterthrush (Parkesia motacilla) along two streams in the Caribbean National Forest in Puerto Rico during 2005–2007. Home range sizes varied with younger birds having larger home ranges and core areas than older birds. All birds occupied some length of stream but a wide range of off-stream habitats were also used. Off-stream habitats included a range of disturbance from residential areas to small saturated pastures. Neighbors exhibited a wide range of overlap in home ranges (x - 20%), and older birds had more overlap than younger birds. The greatest percent of foraging time was along streams (64.4%) followed by muddy substrate (26.5%), housing developments (7.4%), and roads (1.7%). The greater proportion of time foraging along streams indicates this is the preferred habitat for this species, so o o, 2010.

Identifying mechanisms that limit and regulate populations is critical in understanding population dynamics. Identifying these mechanisms for migratory animals is difficult because of the large and often separate geographic areas in which they occur annually (Marra and Holmes 2001). Multiple processes can operate at different times in the annual cycle and in geographically distinct locations. These processes can influence factors that affect population growth rate (i.e., survival and reproduction) including inter- and intra-specific competition, and predation. Most studies of long-distance migratory birds have focused on population regulating mechanisms during the breeding season.

The primary resource requirements for migratory birds during the non-breeding season are food and shelter from predators (Brown and Sherry 2008). Food availability (Sherry and Holmes 1996, Sherry et al. 2005), dominance-mediated habitat segregation (Wunderle 1992, Parrish and Sherry 1994, Marra and Holmes 2001), predator pressure (Watts 1991), and proximity to breeding areas (Cristol et al. 1999, Jenkins and Cristol 2002) affect the distribution of many neotropical migrants during the non-breeding season.

Habitat occupancy during the non-breeding season is an important component of the annual cycle for neotropical migratory birds (Marra et al. 1998); however, empirical data on habitat occupancy and use during the non-breeding season are lacking for most neotropical migrants. Non-breeding occupancy has been shown to affect annual survival (Marra and Holmes 2001), spring migration departure dates, arrival in breeding areas, number of young produced (Reudink et al. 2009), and natal dispersal (Studds et al. 2008).

Neotropical migrants use multiple behavioral strategies including territoriality (Holmes and Sherry 1992, Marra et al. 1993), floating (Brown and Sherry 2008), and joining mixed species flocks (Ewert and Askins 1991, Latta and Wunderle 1996, Gram 1998, Jones et al. 2000, Warkentin and Morton 2000, Potnara et al. 2007) during the non-breeding season. These behavioral strategies may be influenced by gender, food availability (Brown and Sherry 2006), and/or intra-and inter-specific competition which may affect body condition and annual survival.

The Louisiana Waterthrush (Parkesia motacilla), hereafter waterthrush, is a large (19.6 ± 1.4 g) (Mattson et al. 2009), monochromatic neotropical migratory warbler that breeds along first to third order perennial streams in deciduous and evergreen closed-canopy forests at medium to high gradients. They breed in the eastern United States from Wisconsin to central New England in the north to eastern Texas and northern Florida in the south. They overwinter throughout the Caribbean and Central America (Mattson et al. 2009). Waterthrush have been used as indicators of stream integrity (O’Connell et al. 2003). Densities of breeding individuals are reduced along freshwater streams with macroinvertebrate communities compromised by stream acidification and anthropogenic land use changes (Mattsson and
Cooper 2006, Muvihill et al. 2008, Mattsson et al. 2009). The breeding population of the waterthrush has remained stable and/or has slightly increased throughout its range (0.7%/yr, 1966–2007) (Sauer et al. 2008). Waterthrush occur along wooded freshwater streams throughout their non-breeding range (Eaton 1953). Master et al. (2002) suggested they are also riparian specialists during the non-breeding season inhabiting streams with characteristics similar to that of the breeding season.

We examined habitat use and behavioral strategies used by Louisiana Waterthrush during the non-breeding season. Our objectives were to quantify preferred habitat, describe on and off-stream habitat use, and ascertain if age affects habitat use. We made the following predictions: (1) waterthrush are riparian specialists occurring along headwater streams, and (2) they are territorial with older dominant individuals having smaller more resource-rich territories than younger individuals.

METHODS

Study Area.—This study was conducted along the Rio Sabana and a tributary at the northern boundary of the Caribbean National Forest in Sabana, Puerto Rico (18° 46' N, 66° 36' W). The Rio Sabana averages 9.3 m in width along this stretch with an average depth of 21 cm. The stream has riffles and rocks of varying sizes, an average flow rate of 0.20–0.26 m/sec, and a mostly closed canopy of mature trees; some stretches are through a residential part of Sabana. The amount of forest cover surrounding this portion of the watershed varies from contiguous forest to open areas with housing development.

Field Procedures.—Waterthrush were captured between 15 January and 15 February using playback recordings and mist nets placed in highly used flight paths. Birds exhibited low response to playback, and most captures occurred with mist nets placed across streams. All individuals were banded with a unique color band combination (2 color bands and a USGS aluminum band), and classified to age using plumage characteristics (Pyle 1997). No unhanded birds were observed after the capture period was completed. All individuals (n = 22) were fitted with radio transmitters (0.36 g; Model LB-2N, Holohil Systems Ltd., ON, Canada) attached with a cotton string harness to ensure they would degrade prior to spring migration (Hallworth et al. 2009). Home ranges were quantified by collecting a minimum of 50 (Seaman et al. 1999) locations with a Garmin 72 or 76 handheld global positioning system (GPS) (Olathe, KS, USA). Individuals were located via homing and followed for 2 consecutive hours taking locations at 5-min intervals daily for the life of the transmitter (~ 12 days). Five-min sampling intervals were chosen so birds were able to switch between foraging substrates and/or could traverse their home range during this time. Accuracy of home range delineation increases at shorter time intervals, despite the possible autocorrelation that may exist between bird locations (de Solla et al. 1999).

Ground and foraging substrates were quantified within 3-m radius plots at 12 randomly stratified bird locations based on the number of foraging observations within the different habitat types (stream and off stream), as well as six non-use locations created by randomly generated coordinates within individual home ranges. Plots were stratified by categorizing bird observations based on the habitat type used and randomly selected in proportion to use based on the number of total observations. We visually quantified the percent cover of mud, leaf litter, water, and vegetation within each plot. Percent canopy cover was quantified using a densitometer. We measured prey abundance at the center of each vegetation plot within a 1-m radius by recording all arthropods observed for 90 sec and then recording new individuals while turning over litter for an additional 90 sec. All arthropods were identified to Order. All stretches of streams were used, and we were not able to compare use and non-use areas along streams. We classified percent cover of large rock (> 0.5-m diameter), medium rock (> 0.2—< 0.5-m diameter), gravel (rock < 0.2-m diameter), leaf litter (LL), vegetation (Veg), moss, roots and fallen coarse woody debris (Prop), and canopy cover (Canopy) along a 5-m stretch, if randomly stratified plot locations were within the stream. Width (m), flow rate (m/sec) and average depth (cm) of the stream were also quantified.

Statistical Analyses.—We used home range tools for ArcGIS (Rodgers et al. 2007) to calculate fixed-kernel use distributions (UD) from GPS locations for each individual. We used least squares cross validation (LSCV) to ascertain the smoothing parameter value (Barg et al. 2005). Use distributions of 95% were considered an individual’s home range and UD’s of 50% were considered an individual’s core area (Barg et al. 2005).
The areal overlap of home range and core areas was quantified using Hawth’s analysis tools for ArcGIS (Beyer 2004).

Akaike information criterion (AIC), corrected for small sample sizes (AICc; Burnham and Anderson 2001), was used to evaluate models comparing habitat variables between use and non-use areas. We chose seven biologically relevant variables on the basis of field observations which included percent muddy substrate (Mud), percent leaf litter (LL), percent prop roots and fallen coarse woody debris (Fallen), percent canopy cover (Canopy), percent standing/running water (Water), prey availability (Prey), and percent vegetation cover (Veg). Kullback-Leibler information and Akaike’s information criterion, corrected for small sample sizes (AICc) (Burnham and Anderson 2001) were used to evaluate the models. The lowest $\Delta$AICc value indicates the most parsimonious model. Thus, the model with the lowest $\Delta$AICc value indicates goodness-of-fit to the data while minimizing the number of parameters in the model. Binary logistic regressions were calculated with JMP 8.0 (SAS Institute Inc. 2010).

Home range sizes were normally distributed despite low sample sizes (ASY: Shapiro-Wilks' $W = 0.872, df = 13, P = 0.069$; SY: Shapiro-Wilks' $W = 0.972, df = 6, P = 0.907$). Core area size was log transformed to meet the assumptions of normality. Home range and core area size were compared between age classes and location (Rio Sabana or its tributary) with a two-way ANOVA. A Chi-square contingency table was used to examine differences in habitat use between after-second-year (ASY) and second-year (SY) individuals. Arcsine square root transformations were used to normalize data collected as percentages. Prey abundance was log transformed to meet the assumptions of normality. We used $\alpha = 0.05$ for all statistical tests and data are presented as means $\pm$ SE.

RESULTS

Twenty-two waterthrush were tracked during the 3 years, eight in 2005, seven in 2006, and seven in 2007. Fourteen were ASYs, six were SYs, and age of two could not be reliably classified. Males and females have similar plumage and were not distinguishable.

The number of location points obtained per individual ranged from 30 to 206 with a mean of 91.2 $\pm$ 10.6. Home range size varied widely from 0.38 to 8.80 ha. The average home range and core area sizes were 3.03 $\pm$ 0.54 ha and 0.71 $\pm$ 0.14 ha, respectively. ASY (2.15 $\pm$ 0.44 ha) individuals had smaller home ranges than SYs (4.65 $\pm$ 1.24 ha; $F_{1,18} = 8.00, P = 0.013$). Core areas ranged from 0.07 to 2.14 ha. Older individuals (ASYs) had smaller core areas than younger (SY) individuals ($F_{1,18} = 2.55, P = 0.131$) or core area size differed between the Rio Sabana and its tributary when accounting for the age of the individual. The extent of home range overlap varied between 0 and 71.5% with a mean overlap of 20.5 $\pm$ 5.03%. The home ranges of ASYs (24.6 $\pm$ 6.67%) had more overlap than the home ranges of SYs (4.10 $\pm$ 2.20%; $t = 2.31, df = 17, P = 0.03$). The mean percent overlap of core areas was 6.45 $\pm$ 2.66% and did not differ between age classes ($t = 0.92, df = 17, P = 0.37$). Neither the number of overlapping home ranges ($X^2_3 = 3.75, P > 0.05$) nor core area size ($X^2_2 = 2.43, P > 0.05$) differed between ASYs and SYs. The density of waterthrush during the study ranged from three to five individuals/km and was estimated more accurately in our study through use of radio transmitters.

Waterthrush foraged mostly along streams (64 $\pm$ 7%) followed by muddy substrate (27 $\pm$ 6%). A small proportion of the time foraging was in housing developments (7 $\pm$ 5%) or on nearby roads (2 $\pm$ 1%). After-second year individuals spent more time foraging along streams and muddy substrates than expected and avoided...
foraging along roads and in housing developments ($\chi^2_3 = 10.7, P = 0.01$). Second-year individuals spent more time foraging along roads and in housing developments than expected while foraging less along streams and muddy substrates than expected ($\chi^2_3 = 10.7, P = 0.01$).

Mean body condition of individuals did not differ between years (Kruskal Wallis $= 0.95$, df $= 2$, $P = 0.62$). Body condition did not differ between ASYs and SYs (Kolmogorov-Smirnov $Z = 0.936$, $P = 0.35$). Individual body condition was not dependent upon prey availability within their home range ($r^2 = 0.07, t = 0.68, df = 7, P = 0.53$). Prey availability was not correlated with home range ($r = 0.35, t = 1.21, df = 7, P = 0.26$) or core area size ($r = 0.27, t = 0.89, df = 7, P = 0.40$). Body condition was negatively correlated with amount of time foraging along the stream ($r = 0.57, t = 2.56, df = 15, P = 0.02$; Fig. 1).

Body condition was not correlated with amount of time foraging in muddy substrates ($r = 0.07, t = 0.68, df = 7, P = 0.53$). Body condition was not influenced by the size of the home range ($r^2 = 0.12, t = 1.73, df = 14, P = 0.21$) or core area ($r^2 = 0.13, t = 1.50, P = 0.16$) overlap.

Prey availability ($\Delta AIC_c = 0.00$) was the most parsimonious model that distinguished use from non-use locations. Increased prey availability and a lower percent of leaf litter cover ($\Delta AIC_c = 1.82$) also were parsimonious with respect to use and non-use locations (Tables 1, 2). Two additional models that provided moderate support ($2 \leq \Delta AIC_c \leq 4$) included higher percent of muddy substrate and increased prey availability ($\Delta AIC_c = 3.31$), and lower percent of leaf litter cover, higher percent of standing water, and increased prey availability ($\Delta AIC_c = 3.91$). Prey availability ($\Sigma W_r = 1.00$) was the single most important variable that distinguished use from non-use locations. Prey availability was higher along streams and in muddy substrates than non-use locations ($F_2 = 7.9, P = 0.002$; Fig. 2, Table 3). Prey availability did not differ between stream and muddy substrates ($t$-stat $= 0.13, df = 16, P = 0.90$). The entire length of the Rio Sabana and its tributary was used by waterthrush during the study, and we were unable to compare use and non-use stream variables.

**DISCUSSION**

Waterthrush secured fixed home ranges that encompassed multiple habitat types. Home ranges exhibited a wide range of overlap with neighboring individuals although there was minimal overlap of core areas. This overlap did not affect body condition. There was greater overlap among ASYs despite having smaller home ranges. This may be the result of older birds occupying higher quality habitats both along and away from streams. ASYs did not apportion greater percent-

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**TABLE 1.** Habitat variables that characterized use and random non-use locations of foraging Louisiana Waterthrush in the Caribbean National Forest, Puerto Rico. The lowest $\Delta AIC_c$ value indicates the model that best balances goodness-of-fit while minimizing the number of parameters in the model. $W_r$ indicates the weighted model weights. Prey availability and percent leaf litter ($LL_r$) were selected as the two variables that best explain habitat use of Louisiana Waterthrush.

<table>
<thead>
<tr>
<th>Model</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$W_r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey</td>
<td>13.09</td>
<td>0.00</td>
<td>0.54</td>
</tr>
<tr>
<td>LL, Prey</td>
<td>14.91</td>
<td>1.82</td>
<td>0.21</td>
</tr>
<tr>
<td>Mud, Prey</td>
<td>16.40</td>
<td>3.31</td>
<td>0.03</td>
</tr>
<tr>
<td>LL, Water, Prey</td>
<td>17.00</td>
<td>4.91</td>
<td>0.07</td>
</tr>
<tr>
<td>Mud, LL, Prey</td>
<td>18.17</td>
<td>5.08</td>
<td>0.04</td>
</tr>
<tr>
<td>Mud, LL, Water, Prey</td>
<td>20.43</td>
<td>7.33</td>
<td>0.01</td>
</tr>
<tr>
<td>Mud, LL, Water, Prey, Veg</td>
<td>23.05</td>
<td>9.96</td>
<td>0.05</td>
</tr>
<tr>
<td>Mud, LL, Fallen, Canopy, Water, Prey, Veg</td>
<td>27.27</td>
<td>14.18</td>
<td>0.00</td>
</tr>
<tr>
<td>Mud, Canopy, Veg</td>
<td>37.57</td>
<td>24.48</td>
<td>0.00</td>
</tr>
<tr>
<td>Mud, LL, Water, Veg</td>
<td>44.84</td>
<td>31.74</td>
<td>0.00</td>
</tr>
</tbody>
</table>
TABLE 2. Values (x ± SE) measured in 3-m radius plots for mud, leaf litter, water, and vegetation at Louisiana Waterthrush foraging and random non-use locations presented as percent ground cover in the Caribbean National Forest, Puerto Rico.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mud</th>
<th>Leaf Litter</th>
<th>Water</th>
<th>Vegetation</th>
<th>Canopy</th>
<th>Prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Use</td>
<td>38.8 ± 4.89</td>
<td>43.5 ± 4.12</td>
<td>11.7 ± 2.69</td>
<td>47.9 ± 3.60</td>
<td>87.0 ± 3.11</td>
<td>8.04 ± 0.73</td>
</tr>
<tr>
<td>Non-use</td>
<td>1.04 ± 0.58</td>
<td>91.7 ± 1.99</td>
<td>3.13 ± 2.92</td>
<td>48.1 ± 5.07</td>
<td>94.7 ± 0.35</td>
<td>5.26 ± 1.24</td>
</tr>
</tbody>
</table>

When individuals crossed paths, these encounters were only observed along streams (MTH, pers. obs.). Waterthrush, like Ovenbirds (Seuirus auricapilla), may maintain and defend smaller territories through active defense of core areas and during chance encounters with conspecifics (Brown and Sherry 2008). ASYs had significantly smaller home ranges than SYs also suggesting older individuals are able to secure higher quality home ranges (Holmes et al. 1996); however, neither home range nor core area size was correlated with prey availability. Roost sites (Smith et al. 2008) and cover (Watts 1991) may also influence home range size.

Waterthrush mostly foraged along streams but also used off-stream habitats with appropriate ground substrate, especially in areas with concentrated arthropod abundance. The most important ground feature in off-stream areas used for foraging was the amount of muddy substrate. Foraging locations had nearly 40% muddy ground cover compared to 1% in non-use areas. Northern Waterthrush (Parkesia noveboracensis) and Louisiana Waterthrush seek saturated soils that are often rich in arthropods (Smith et al. 2010). Foraging locations had less than half the leaf litter compared to non-use areas. There was nearly four times greater standing water and greater prey abundances in areas used for foraging. Waterthrush are ground foragers and attracted to moist substrates. Thus, when not along streams they seek areas where ground arthropods are in higher concentrations. Prey availability was the most parsimonious model that influenced habitat use, followed by a model containing prey availability and percent leaf litter. The importance of leaf litter is likely due to waterthrush actively searching for arthropods by flipping leaves as they forage both on and off stream (MTH, LRR, pers. obs.).

Individual body condition was negatively correlated with amount of time foraging along the stream which may be influenced by the amount of conspecific encounters and time spent defending core areas. Conspecific encounters and aggression were only observed along streams (MTH, LRR, pers. obs.). The riparian habitat in this study area has been affected by development which may have impacted water quality and stream invertebrate richness and abundance. The streams still attract waterthrush, but they may not have suitable conditions for invertebrate productivity.

Return rates (13–29%) in our study were low for a neotropical migrant when compared to
Prairie Warbler (*Dendroica discolor*) (50%) (Latta and Faaborg 2001), American Redstart (*Setophaga ruticilla*) (40–70%) (Marra and Holmes 2001), and Northern Waterthrush (14–52%) (Reitsma et al. 2002) during the non-breeding season. It was not possible to discern mortality from emigration. Use of radio transmitters may be a cause for the low return rates (see Mattson et al. 2006), but 59% of the birds with transmitters were recaptured and harnesses removed prior to spring departure. Use of cotton string as a harness increases the probability that transmitters are lost within 4–6 weeks of application, prior to migration (Hallworth et al. 2009). Previous work on Louisiana Waterthrush during the non-breeding season suggests this species is a riparian specialist with similar habitat requirements to those used during the breeding season (Master et al. 2002). Our study suggests Louisiana Waterthrushes are not strictly associated with headwater streams and use a variety of habitat types including muddy substrates and housing developments. Food availability influenced habitat use of individuals although it did not appear to impact home range size or core area. Water quality parameters were not measured although Master et al. (2002) found the highest waterthrush densities (10 individuals/km) in Costa Rica occurred along streams with moderate to high abundance of macroinvertebrates. Waterthrush use areas as far as 150 m from streams despite being closely associated with riparian habitats. Our study illustrates the importance of food availability for Louisiana Waterthrush and indicates this species uses a wider array of habitat types than previously thought. The frequent use of saturated soils adjacent to rivers and streams as foraging sites is an important component to understanding their non-breeding distribution and, potentially, for considering this species’ conservation throughout their wintering distribution.

**ACKNOWLEDGMENTS**

We thank J. M. Wunderle and J. E. Mercado for support and assistance as well as the staff at Sabana Field Station, Sabana, Puerto Rico. The authors also thank P. M. Benham, A. J. Leppold, R. S. Mulvihill, F. L. Newell, and Carly Reitsma for help in the field. This study was supported by the New England Institute for Landscape Ecology. We thank C. E. Braun and two anonymous reviewers who made comments that improved this paper.

**LITERATURE CITED**


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SPRING STOPOVER AND REFUELING AMONG MIGRANT PASSERINES IN THE SIERRA DE LOS TUXTLAS, VERACRUZ, MEXICO

DAVID W. SHAW1,2,3 AND KEVIN WINKER1

ABSTRACT.—The narrowing of the North American continent at the Isthmus of Tehuantepec creates an important geographic bottleneck for songbirds on their northward spring migrations. The Sierra de Los Tuxtlas, in the northwestern portion of the Isthmus, provide an ideal location from which to address questions of resource use and fuel acquisition during migration. We operated mist nets during morning and evening to capture passerines during spring migration in 2004 and 2005. Seven of 13 taxa had significant diurnal increases in body condition (an index of size-adjusted mass): Swainson’s Thrush (Catharus ustulatus), Wood Thrush (Hylocichla mustelinea), Magnolia Warbler (Dendroica magnolia), Kentucky Warbler (Oporornis formatus), Hooded Warbler (Wilsonia citrina), Worm-eating Warbler (Helmitheros vermivorum), and Ovenbird (Seiurus aurocapilla). All of these species, except Ovenbird, also had a significant increase in fat score. Indigo Buntings (Passerina cyanea) had a significant increase in fat score but not in condition index. A comparison with autumn migration at this site showed overall similarities in percentage of species gaining mass and in the amount gained, but there were seasonal differences within species. There was no relationship between increase in body condition and a mainland versus trans-gulf migratory strategy. Received 13 November 2007. Accepted 19 March 2011.

Migration places intense physical demands on birds. One of the main adaptations enabling birds to make long-distance seasonal migrations is fat deposition (Blem 1990, Rogers 1991). Food resources at stopover locations are likely critical and, because the geography of Middle America causes a relatively rapid latitudinal decline in available space for landbirds migrating south in autumn, competition for food resources may be high. Land availability for these birds during spring migration increases rapidly north of the Isthmus of Tehuantepec. Several studies have addressed refueling and stopover ecology during autumn on this isthmus and farther south in Middle America (Galindo et al. 1963; Galindo and Mendez 1965; Rogers and Odum 1966; Child 1969; Winker 1995a, b; Johnson and Winker 2008), but there are few reports of work conducted in spring (e.g., Galindo et al. 1963, Wilson et al. 2008).

Our field site in the Sierra de Los Tuxtlas in the northwestern portion of the Isthmus of Tehuantepec, Mexico, provides an ideal location from which to study refueling strategies and stopover ecology among migrant songbirds. The ecology of migrating birds in this region is only beginning to be understood (Rappole and Warner 1980; Rappole 1995; Winker 1995a, b). This site was used previously to investigate refueling by autumn migrants (Winker 1995a), which permits direct comparisons of seasonal refueling strategies. Our objectives were to gather data on fat levels and mass gains among the common, nocturnally migrating passerines passing through Los Tuxtlas during spring migration to understand seasonal and geographic patterns of fuel deposition and route selection in this region. Specifically, we collected data during two migratory seasons to address four questions. (1) What quantity of fat do spring migrants carry through this region? (2) Do they show a net gain in fuel during stopover? (3) Are there differences in how this site is used for refueling between spring and autumn? (4) What can be inferred about route selection in this region?

METHODS

Study Area.—We conducted fieldwork in the Sierra de Los Tuxtlas (Fig. 1) in southern Veracruz, Mexico, 90 km southeast of Veracruz city. This range of mountains is in the northwestern portion of the Isthmus of Tehuantepec and is isolated from the Sierra Madre Oriental by extensive lowlands. The Los Tuxtlas region encompasses ~4,200 km² and is dominated by Volcan San Martin and Volcan Santa Marta, each reaching >1,500 m in elevation. The Gulf of Mexico is a short distance from the mountains to the north and east. Habitat in the region was formerly dominated by the farthest north neotropical evergreen rain forest but, due to deforestation,
FIG. 1. Mexico and Central America indicating location of field site in the Sierra de Los Tuxtlas, Mexico.

it is now a mosaic with a high percentage of pasture, fence rows, and isolated trees (Dirzo and Garcia 1992). Andrle (1964) estimated that 50% of the region was forested in 1962; by 1986 15% of forests remained (Winker et al. 1990, Dirzo and Garcia 1992), and in 1994 only 7-10% of the region was forested (Winker 1997). The remaining forest is primarily in the highlands and is scarce below 500 m above sea level (Rappole et al. 1994).

Our field site is on the southern edge of the 700-ha Estacion de Biologia Los Tuxtlas (18° 34' 30" N, 95° 04’ 20" W) operated by the Instituto de Biologia at the Universidad Nacional Autonoma de Mexico. The field station protects one of the few remaining large tracts of lowland evergreen forest in the region. The climate is hot and wet with a mean annual temperature of 25°C (Soto and Gama 1997). Annual precipitation is 4.5–4.9 m with a short drier season from March to May (Soto and Gama 1997). Our netting site was on the edge of the Estacion in primary and second-growth forests ~150 m above sea level. The exact netting site was used previously by Winker (1995a), and we placed nets as precisely as possible in the same net lanes. Canopy heights in the primary forest ranged from 30 to 35 m (Ibarra-Manriquez et al. 1997). Second growth areas had variable canopy heights from 3 to 20 m.

Data Collection.—Thirty-six standard nylon mist nets (12 X 2.6 m, 30 and 36 mm mesh) were placed 30 m apart in primary and second-growth forest and operated (weather permitting) during daylight hours. The outer rows of nets encompassed an area of ~1.8 ha. Effort was concentrated in the morning and evening. Nets were open for 8,395 net hrs between 21 February and 27 April 2003 and for 2,312 net hrs from 5 to 29 April 2004. We placed captured birds in light cloth bags and brought them to a central processing area. Birds were banded, wing chord and tail lengths were measured to the nearest 0.1 mm using vernier calipers, and birds were weighed to the nearest 0.1 g using Pesola spring scales. Fat scores were assigned following Helms and Drury (1960).

Data Analyses.—T-tests were used to examine gross differences in overall condition (mass/wing chord × 100) between years. We pooled data from both field seasons because only Hooded
We selected 2003 for analyses for the Hooded Warbler (Wilsonia citrina) had a significant difference between years ($t = 1.99$, $P = 0.013$).

We selected 2003 for analyses for the Hooded Warbler to avoid confounding analyses with apparent between-year differences; 2003 had the larger sample (2003: 171 vs. 2004: 36). Twelve migrant species and the genus Empidonax had sufficient numbers of captures for analyses ($n \geq 30$; Table 1). We pooled data for Least Flycatcher (Empidonax minimus) and ‘Trail II’ flycatchers (E. alnorum and E. traillii) to increase sample size sufficiently for Empidonax flycatchers to be included in analyses (this may have included a few Empidonax virescens, although we had no specimens). The Empidonax group is hereafter referred to as one of the study ‘species.’ One of our goals was to contrast migrants at this site in spring with the same site in autumn; thus, we followed Winker (1995a) in analytical assumptions and in including all first captures, which for some species may include a small number of locally wintering birds. We reduced the likelihood of including these in three ways. (1) Early-season captures of overwintering species were banded and excluded. (2) The site is small, most of these species are territorial in winter and, if step one missed a few birds, they were numerically swamped by passage migrants. (3) We focused netting during 2004 on the period of greatest migrant movement through this area.

Our method of quantitatively estimating mass gains among stopover migrants assumes that birds foraging in a suitable environment will have a diurnal mass increase from food intake and fuel deposition with subsequent loss at night due to fasting, nocturnal metabolism, and excretion of undigestible material. Non-foraging individuals, or those in an unsuitable environment, will show a diel or 24-hr mass decrease. We created a ‘condition index’ for each first-time capture by dividing mass by wing chord and multiplying this value by a constant (100). Wing chord has been shown to be an appropriate proxy for size (Winker et al. 1992a, Winker 1995a). We then regressed condition index on time of day of capture (first captures only) to examine whether there was diurnal increase in condition, averaged across all sampling days. This technique follows Winker et al. (1992a) and Winker (1995a) and examines species-level trends. Body mass is the most important variable, and inclusion of a size-related variable in the condition index somewhat corrects for size differences among individuals. (Linear regressions of wing chord on time of day showed no significant relationships for any species examined.) Mass has been shown in fat-free mass studies to correlate with fat carried (Rogers 1965, Rogers and Odum 1966). The underlying assumption is that condition index is correlated with amount of fuel carried.

We used fat scores, gauged from visible furcular and abdominal fat, to corroborate evidence for trends observed in condition indices (Winker 1995a, Dunn 2002). Fat scores are somewhat qualitative and subject to variation between observers, and are not suitable for

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean time of capture</th>
<th>Mass, g</th>
<th>Wing chord, mm</th>
<th>Tail, mm</th>
<th>Fat score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empidonax spp.</td>
<td>35</td>
<td>1111</td>
<td>11.8 (4.91)</td>
<td>66.5 (7.75)</td>
<td>55.5 (5.07)</td>
</tr>
<tr>
<td>Gray-cheeked Thrush (Catharus minimus)</td>
<td>58</td>
<td>1157</td>
<td>27.1 (3.14)</td>
<td>98.8 (3.78)</td>
<td>69.1 (4.52)</td>
</tr>
<tr>
<td>Swainson’s Thrush (C. ustulatus)</td>
<td>323</td>
<td>1147</td>
<td>30.8 (3.40)</td>
<td>95.5 (5.68)</td>
<td>66.2 (3.52)</td>
</tr>
<tr>
<td>Wood Thrush (Hylocichla mustelina)</td>
<td>120</td>
<td>1118</td>
<td>47.6 (5.99)</td>
<td>100.0 (14.73)</td>
<td>67.7 (3.39)</td>
</tr>
<tr>
<td>Gray Catbird (Dumetella carolinensis)</td>
<td>38</td>
<td>1129</td>
<td>35.1 (2.62)</td>
<td>86.9 (2.65)</td>
<td>89.8 (3.83)</td>
</tr>
<tr>
<td>Magnolia Warbler (Dendroica magnolia)</td>
<td>39</td>
<td>1212</td>
<td>7.9 (0.83)</td>
<td>57.5 (2.07)</td>
<td>47.2 (2.11)</td>
</tr>
<tr>
<td>Kentucky Warbler (Oporornis formosus)</td>
<td>136</td>
<td>1151</td>
<td>13.4 (1.67)</td>
<td>65.0 (2.60)</td>
<td>46.8 (2.41)</td>
</tr>
<tr>
<td>Hooded Warbler (Wilsonia citrina)</td>
<td>171</td>
<td>1132</td>
<td>11.0 (2.93)</td>
<td>61.9 (3.98)</td>
<td>53.8 (4.23)</td>
</tr>
<tr>
<td>Worm-eating Warbler (Helmitheros vermivorum)</td>
<td>78</td>
<td>1124</td>
<td>13.7 (1.52)</td>
<td>66.7 (2.91)</td>
<td>47.7 (2.36)</td>
</tr>
<tr>
<td>Yellow-breasted Chat (Icteria virens)</td>
<td>43</td>
<td>1042</td>
<td>26.4 (2.81)</td>
<td>73.6 (2.53)</td>
<td>71.4 (3.76)</td>
</tr>
<tr>
<td>Ovenbird (Seiurus aurocapilla)</td>
<td>68</td>
<td>1125</td>
<td>18.5 (1.81)</td>
<td>72.7 (2.62)</td>
<td>51.6 (1.83)</td>
</tr>
<tr>
<td>Parnell Bunting (Passerina ciris)</td>
<td>31</td>
<td>1013</td>
<td>15.8 (1.89)</td>
<td>69.4 (2.67)</td>
<td>53.8 (2.46)</td>
</tr>
<tr>
<td>Bullock Bunting (P. caerulea)</td>
<td>159</td>
<td>1111</td>
<td>15.2 (4.57)</td>
<td>65.7 (4.94)</td>
<td>50.0 (3.39)</td>
</tr>
</tbody>
</table>

TABLE 1. Sample sizes and quantified variables with means (SD) for 13 taxa captured during spring 2003 and 2004 in the Sierra de Los Tuxtlas, Mexico. (Hooded Warblers are for 2003 only).
quantitative estimates of gains. Standard linear
regressions may not be appropriate due to the
categorical nature of fat scores; but they have
been used in other studies (e.g., Dunn 2001, 2002;
Johnson and Winker 2008) and have heuristic and
comparative value. We conducted both linear and
ordinal regressions to examine whether using an
ordinal regression would yield different results.
We regressed fat scores on time of capture using
both methods.

We compared (at the species level) estimated
daily gains with an estimated distance of migration
to determine if this pattern was affected by
migration distance. We used linear regression to
calculate the slopes of the gain scores against the
distance to the middle of each species' breeding range.
We also regressed fat scores on time of day
(excluding Winker 1992b). Total 24-hr mass gains
were estimated by subtracting nocturnal losses
from the estimated average diurnal increase. We
used both linear and ordinal regression to examine
whether a relationship was present between time of
day on the site and refueling. The number of hours and
distance that the average captured individual was
capable of flying were estimated using the
average species-level diet-gain rates, rates of energy
use during migration (Tucker 1974), and
published values for the energetic content of fat and
flight speed: 30.2 kJ/g (Pennycuick 2003) and
40.7 km/hr (Nisbet et al. 1963). We arcsine
transformed the data and used linear regression due to the
apparently linear nature of the data.

Percentages of species recaptured after a night or
more at the site were regressed against slopes of
the condition index regression to examine whether a relationship was present between time of
day on the site and refueling. The number of hours and
distance that the average captured individual was
capable of flying were estimated using the
average species-level diet-gain rates, rates of energy
use during migration (Tucker 1974), and
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transformed the data and used linear regression due to the
apparently linear nature of the data.

Percentages of species recaptured after a night or
more at the site were regressed against slopes of
the condition index regression to examine whether a relationship was present between time of
day on the site and refueling. The number of hours and
distance that the average captured individual was
capable of flying were estimated using the
average species-level diet-gain rates, rates of energy
use during migration (Tucker 1974), and
published values for the energetic content of fat and
flight speed: 30.2 kJ/g (Pennycuick 2003) and
40.7 km/hr (Nisbet et al. 1963). We arcsine
transformed the data and used linear regression due to the
apparently linear nature of the data.

Percentages of species recaptured after a night or
more at the site were regressed against slopes of
the condition index regression to examine whether a relationship was present between time of
day on the site and refueling. The number of hours and
distance that the average captured individual was
capable of flying were estimated using the
average species-level diet-gain rates, rates of energy
use during migration (Tucker 1974), and
published values for the energetic content of fat and
flight speed: 30.2 kJ/g (Pennycuick 2003) and
40.7 km/hr (Nisbet et al. 1963). We arcsine
transformed the data and used linear regression due to the
apparently linear nature of the data.

Results

Swainson's Thrushes, Wood Thrushes (Hylocichla mustelina), Hooded Warblers, Magnolia Warblers (Dendroica magnolia), Kentucky Warblers (Oporornis formosus), and Ovenbirds (Seiurus aurocapilla) had significant positive
slopes in condition index (Table 2, Fig. 2). No
species had significant negative slopes. Diurnal
condition slopes did not differ significantly from zero in six taxa: Empidonax, Gray-cheeked
Thrushes (Catharus minimus), Gray Catbirds
(Dumetella carolinensis), Worm-eating Warblers
(Helminthis vermicularis), Yellow-breasted
Chats (Icteria virens), Painted Buntings (Paspur-
tina ciris), and Indigo Buntings (P. cyanus).

Both linear and ordinal regressions of fat scores
on time of day indicated the same species had
significant gains. These results corroborated the
observed increases in condition index. Only the
Ovenbird had significant diurnal condition gains
but did not have corresponding diurnal increases
in fat score. The Indigo Bunting did not have
positive condition gains but had a significant
increase in fat score (Table 2). A considerable
percentage of Indigo Buntings (34%), Magnolia
Warblers (34%), and Empidonax flycatchers
(36%) had some body molt. This additional

RESULTS
TABLE 2. Regression of condition index (1) and fat score (2) on time of capture and migration strategy for 13 taxa captured during spring migration in the Sierra de Los Tuxtlas, Mexico. All significant regressions were positive; regression slopes are in Table 3.

<table>
<thead>
<tr>
<th>Species</th>
<th>Condition index</th>
<th>Fat score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( r^2 )</td>
<td>( F )</td>
</tr>
<tr>
<td>Empidonax spp.</td>
<td>0.071</td>
<td>2.36</td>
</tr>
<tr>
<td>Gray-cheeked Thrush</td>
<td>0.005</td>
<td>0.28</td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>0.038</td>
<td>12.10</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>0.088</td>
<td>11.06</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>0.003</td>
<td>0.09</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>0.130</td>
<td>5.39</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>0.048</td>
<td>6.59</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>0.063</td>
<td>11.33</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>0.058</td>
<td>4.62</td>
</tr>
<tr>
<td>Yellow-breasted Chat</td>
<td>0.007</td>
<td>0.31</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>0.057</td>
<td>4.01</td>
</tr>
<tr>
<td>Painted Bunting</td>
<td>0.002</td>
<td>0.05</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>0.009</td>
<td>1.34</td>
</tr>
</tbody>
</table>

Energetic demand may limit the amount of fat individuals can carry and their ability to refuel. Of these three species, Magnolia Warblers had a significant positive increase in both body condition and fat score throughout the day, and Indigo Buntings had significant positive diurnal gains in fat score.

Diurnal mass gains were estimated for the seven species with non-zero trends in condition index. Subtracting estimated nocturnal losses gave an estimate of average mass gain over a 24-hr period. Mass gain estimates varied from 2.8 to 7.7% of a species’ average body mass (Table 3). No species had a net loss in condition. Estimated gains were lowest for Swainson’s Thrush (2.8% of mean body mass) and highest for Wood Thrush (7.7%; Table 3).

Nine of the 10 species in our study for which fat-free mass data were available (mean, sample size, min-max, and SD) were significantly heavier than fat-free mass (Table 4). Only Magnolia Warblers were not significantly different. However, the lack of visible fat does not preclude the presence of internal or blood-borne fat (extracted by Odum, in Dunning 1993), and fat scoring is subject to variation (Krementz and Pendleton 1990; Table 5). However, use of fat-free estimates based on fat scores provides a second useful method for estimating the amount of fat available for migration.

There was no relationship between refueling level and migration distance from Los Tuxtlas to the center of the breeding range \( (F = 0.271, P = 0.62) \). There was a significant negative correlation between average amount of fuel carried and extent of refueling observed for the seven species with significant diel gains (arcsine transformed data; \( F = 10.31, P = 0.024 \); Fig. 3). A significant relationship was found \( (r^2 = 0.399, F = 7.289, P = 0.021) \) when percent of recaptures (after 24 hrs; Table 6) was regressed against the slopes of the condition index regressions for all study species (Table 3). This indicates that species with a higher proportion of individuals spending more than 1 day on the site refuel more than those with higher rates of daily departure (Table 6).

Flight capacities were estimated for those species for which fat-free mass data were available. The average individual of these species was capable of between 2 and 7 hrs of flight after a single day’s foraging (Table 7). Total flight distances, assuming still air and exhaustion of all fuel reserves, would allow a range of 323 to 674 km, depending on species (Table 7). These distances are clearly insufficient for a trans-gulf flight in still air of 1,150 km departing from Los Tuxtlas to Galveston, Texas. These distances are substantially reduced, from 66 to 425 km, when using flight capacity estimates based on the average mass of individuals with zero fat score, as are the number of individuals capable of completing a trans-gulf flight to Galveston (Table 8). The average mass of Gray-cheeked Thrushes with zero fat score, perhaps due to geographic variation in body size,
FIG. 2. Condition and fat indices regressed against time for Kentucky Warblers captured during spring migration, 2003 and 2004, in the Sierra de Los Tuxtlas, Mexico (condition: $n = 133, r^2 = 0.05, P = 0.004$; fat index: $n = 133, r^2 = 0.065, P = 0.003$) showing the best linear model.
TABLE 3. Change in mass, indicating slope (m), diurnal gain (g) based on a 12.5-hr day, nocturnal loss (g) based on 4.5% of species' mean mass, estimated 24 hr net gain (g), and percentage of the species' average mass in the Sierra de Los Tuxtlas, Mexico in spring.

<table>
<thead>
<tr>
<th>Species</th>
<th>m</th>
<th>Diurnal gain</th>
<th>Nocturnal loss</th>
<th>Net gain/day</th>
<th>% of mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swainson’s Thrush</td>
<td>0.00188</td>
<td>2.243</td>
<td>1.386</td>
<td>0.858</td>
<td>2.79</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>0.00465</td>
<td>5.813</td>
<td>2.141</td>
<td>3.671</td>
<td>7.72</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>0.00146</td>
<td>1.046</td>
<td>0.411</td>
<td>0.634</td>
<td>6.94</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>0.00171</td>
<td>1.393</td>
<td>0.601</td>
<td>0.791</td>
<td>5.92</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>0.00118</td>
<td>0.913</td>
<td>0.488</td>
<td>0.424</td>
<td>3.91</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>0.00150</td>
<td>1.253</td>
<td>0.615</td>
<td>0.638</td>
<td>4.67</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>0.00156</td>
<td>1.418</td>
<td>0.831</td>
<td>0.587</td>
<td>3.18</td>
</tr>
</tbody>
</table>

sex ratios, or unknown factors, was 0.7 g less than the fat-free mass. The average mass of individuals with fat scores of zero for all other species was greater than the fat-free mass.

We examined the proportion of the sample population capable of completing a trans-gulf flight in still air by calculating the amount of fuel necessary for each species using both techniques for estimating fuel content and comparing it to the estimated amount of fuel carried by each individual (Table 8). Percentages of the populations of study species capable of the flight varied from 0 to 15.4% using a base of fat-free mass, and from 0 to 9% using a base of zero-fat score individuals. Hooded Warblers had the most dramatic difference between the two techniques (13.5 vs. 0%), whereas some species varied little or none.

We used ANOVA comparing the standard errors of the regressions to ascertain whether single-route migrants fattened differently than dual-route migrants; this test failed to show significant differences between groups ($F = 0.144$, $P = 0.932$).

DISCUSSION

The majority of migrant passerines in our study carried substantial quantities of fat. Nine of the 10 study species that were comparable with Odum (in Dunning 1993) had an average body mass significantly greater than fat-free mass. The amount of fuel estimated varied from 7 to 23% of live mass. Eight of the 13 study taxa had significant diel gains in either body condition or fat score. However, neither diel gains nor total fat carried (Tables 5, 7) were sufficient for the average individual of any species to cross the Gulf of Mexico from Los Tuxtlas in still air (Fig. 4). A lack of power due to small sample sizes cannot fully explain why some but not all taxa had significant gains. Species such as Yellow-breasted Chat and Gray-cheeked Thrush did not have any indication of change in diurnal condition or fat score trends despite substantial sample sizes (Tables 1, 2).

Body molt was noted in three taxa; two had significant diel gains either in condition index or fat score. Molt places additional energetic de-

TABLE 4. Comparison of fat-free mass (from Odum in Dunning 1993) to mean mass of study species captured in spring in the Sierra de Los Tuxtlas, Mexico using two-sample $t$-tests.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fat free mass (g)</th>
<th>Tuxtlas mass (g)</th>
<th>Difference (g)</th>
<th>% of live mass</th>
<th>$t$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gray-cheeked Thrush</td>
<td>25.30</td>
<td>27.13</td>
<td>1.93</td>
<td>7</td>
<td>3.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>24.18</td>
<td>30.79</td>
<td>6.61</td>
<td>21</td>
<td>28.89</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>42.21</td>
<td>47.54</td>
<td>5.33</td>
<td>11</td>
<td>8.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>31.80</td>
<td>35.09</td>
<td>3.29</td>
<td>9</td>
<td>6.94</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>6.92</td>
<td>7.89</td>
<td>0.97</td>
<td>12</td>
<td>0.75</td>
<td>ns</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>11.36</td>
<td>13.38</td>
<td>2.02</td>
<td>15</td>
<td>13.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>8.20</td>
<td>10.60</td>
<td>2.40</td>
<td>23</td>
<td>22.63</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>10.79</td>
<td>13.62</td>
<td>2.83</td>
<td>21</td>
<td>12.08</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>15.52</td>
<td>18.55</td>
<td>3.03</td>
<td>16</td>
<td>10.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>12.34</td>
<td>14.70</td>
<td>2.36</td>
<td>16</td>
<td>14.58</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
TABLE 5. Flight capacity estimates based on birds captured in the Sierra de Los Tuxtlas, Mexico presenting mean mass of zero fat score birds, sample sizes and standard deviations, estimated fat, and maximum hours and distances possible assuming all mass greater than the average when fat score is zero is fuel that could be used for migration.

<table>
<thead>
<tr>
<th>Species</th>
<th>Tuxtlas zero fat score (n, SD)</th>
<th>Estimated fat (g)</th>
<th>Maximum hrs of flight</th>
<th>Maximum flight distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empidonax spp.</td>
<td>10.81 (12, 1.09)</td>
<td>1.02</td>
<td>6.85</td>
<td>279</td>
</tr>
<tr>
<td>Gray-cheeked Thrush</td>
<td>24.50 (5, 2.81)</td>
<td>2.63</td>
<td>7.86</td>
<td>320</td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>26.84 (16, 2.13)</td>
<td>3.95</td>
<td>10.44</td>
<td>425</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>42.29 (13, 4.81)</td>
<td>5.25</td>
<td>9.09</td>
<td>370</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>34.39 (7, 2.70)</td>
<td>0.70</td>
<td>1.63</td>
<td>66</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>7.64 (7, 0.85)</td>
<td>0.34</td>
<td>3.38</td>
<td>138</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>11.99 (37, 0.85)</td>
<td>1.39</td>
<td>8.27</td>
<td>337</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>9.52 (28, 0.68)</td>
<td>1.08</td>
<td>8.07</td>
<td>328</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>11.86 (8, 1.00)</td>
<td>1.76</td>
<td>10.30</td>
<td>419</td>
</tr>
<tr>
<td>Yellow-breasted Chat</td>
<td>23.00 (1, n/a)</td>
<td>3.38</td>
<td>10.39</td>
<td>423</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>17.59 (21, 2.09)</td>
<td>0.96</td>
<td>4.16</td>
<td>169</td>
</tr>
<tr>
<td>Painted Bunting</td>
<td>15.44 (4, 0.71)</td>
<td>0.37</td>
<td>1.87</td>
<td>76</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>13.66 (33, 1.24)</td>
<td>1.51</td>
<td>7.95</td>
<td>324</td>
</tr>
</tbody>
</table>

mands on migrating birds, but it did not appear to prevent net fuel gains at this site; examination of the percentage of individuals molting in a species versus the estimated diel mass gain showed no relationship (not shown).

Spring vs. Autumn.—Sandberg (1996) and Sandberg and Moore (1996) hypothesized that resource uncertainty and the impending breeding season would cause spring migrants to fatten more dramatically during migration through more northern latitudes than in autumn. Winker (1995a) proposed this same pattern might be found at the Los Tuxtlas stopover site. However, the percentage of species with significant refuel-

![Graph](image-url)  
**FIG. 3.** Regression of percent of mass carried above fat-free mass (estimated from Odum in Dunning 1993) vs. estimated percent of mass (based on g of fuel from Table 1) gained during the day in the Sierra de Los Tuxtlas, Mexico for the seven migrant species showing significant positive increases in body condition ($r^2 = 0.675, P = 0.023$).
TABLE 6. Total captures, numbers and percent of individuals recaptured > 1 night after initial capture, and numbers and percent of individuals recaptured > 2 nights after initial capture in the Sierra de Los Tuxtlas, Mexico.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total captures</th>
<th>Recaptures (n)</th>
<th>Percent recaptured</th>
<th>Recaptured after 48 hrs (n)</th>
<th>Percent recaptured after 48 hrs</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Empidonax</em> spp.</td>
<td>35</td>
<td>2</td>
<td>5.7</td>
<td>2</td>
<td>5.7</td>
</tr>
<tr>
<td>Gray-cheeked Thrush</td>
<td>58</td>
<td>3</td>
<td>5.2</td>
<td>1</td>
<td>1.7</td>
</tr>
<tr>
<td>Swainson's Thrush</td>
<td>323</td>
<td>20</td>
<td>6.2</td>
<td>9</td>
<td>2.8</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>120</td>
<td>26</td>
<td>21.7</td>
<td>15</td>
<td>12.5</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>38</td>
<td>1</td>
<td>2.6</td>
<td>1</td>
<td>2.6</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>39</td>
<td>4</td>
<td>10.3</td>
<td>4</td>
<td>10.3</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>136</td>
<td>25</td>
<td>18.4</td>
<td>22</td>
<td>16.2</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>171</td>
<td>42</td>
<td>24.6</td>
<td>30</td>
<td>17.5</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>78</td>
<td>17</td>
<td>21.8</td>
<td>12</td>
<td>15.4</td>
</tr>
<tr>
<td>Yellow-breasted Chat</td>
<td>43</td>
<td>3</td>
<td>7.0</td>
<td>2</td>
<td>4.7</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>68</td>
<td>19</td>
<td>27.9</td>
<td>14</td>
<td>20.6</td>
</tr>
<tr>
<td>Painted Bunting</td>
<td>31</td>
<td>2</td>
<td>6.5</td>
<td>1</td>
<td>3.2</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>159</td>
<td>5</td>
<td>3.1</td>
<td>4</td>
<td>2.5</td>
</tr>
</tbody>
</table>

ing was not different between seasons at this site: six of 11 species (55%) in Winker (1995a) and seven of 13 species (54%) in this study. Diet gains, estimated using identical assumptions (Winker 1995a), were remarkably similar among species gaining mass at this site, averaging 5.1% in autumn (Winker 1995a) versus 5.0% in spring. Species that had significant gains differed between seasons but, in spring, no species had a net loss in condition as occurred on the site during autumn (Winker 1995a).

Winker (1995a) detected no significant diel condition increases in Wood Thrushes, Hooded Warblers, and Ovenbirds at this site in autumn, but each had significant increases at the same site during spring. All three of these species winter in large numbers in Los Tuxtlas and surrounding regions. It is likely that many individuals captured in autumn were arriving on or near their wintering areas and had no need to refuel. In spring, these species are embarking on migration and/ or arriving from areas to the south, and the need for refueling may be greater. However, Gray Catbirds also winter at Los Tuxtlas, and Winker (1995a) detected significant autumn diel gains in this species where none was apparent in spring. The reasons for seasonal differences remain unclear.

**Route Selection.**—Migrants at this site were carrying insufficient fuel for long-distance flight. Trans-gulf migrants should be expected to demonstrate higher levels of refueling or to remain

TABLE 7. Flight capacity estimates for average individuals of the study species indicating cost of flight (g of fuel/hr), maximum hours possible based on a single day in the Sierra de Los Tuxtlas, Mexico, and estimates for maximum hours and distances possible.

<table>
<thead>
<tr>
<th>Species</th>
<th>Flight cost (g/hr)</th>
<th>Hours of flight daily gains</th>
<th>Maximum hrs of flight</th>
<th>Maximum flight distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gray-cheeked Thrush</td>
<td>0.33</td>
<td>NA</td>
<td>5.78</td>
<td>235</td>
</tr>
<tr>
<td>Swainson's Thrush</td>
<td>0.38</td>
<td>2.26</td>
<td>17.47</td>
<td>711</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>0.58</td>
<td>6.33</td>
<td>9.22</td>
<td>375</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>0.43</td>
<td>NA</td>
<td>7.66</td>
<td>312</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>0.10</td>
<td>6.34</td>
<td>9.68</td>
<td>394</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>0.17</td>
<td>3.75</td>
<td>16.56</td>
<td>674</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>0.17</td>
<td>4.65</td>
<td>12.04</td>
<td>490</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>0.13</td>
<td>3.26</td>
<td>17.90</td>
<td>792</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>0.23</td>
<td>2.55</td>
<td>13.12</td>
<td>534</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>0.18</td>
<td>NA</td>
<td>12.83</td>
<td>522</td>
</tr>
</tbody>
</table>

* Based on calculations from Tucker (1974).
* Capacity estimates based on 30.2 kJ/g of fuel (Pennycuick 2003).
* Calculated by subtracting average mass from average fat-free mass (from Odum Is Dunting 1993) and assuming difference is fuel.
* Assuming average speed of 40.3 km/hr for an average Swainson’s Thrush (Nisbet et al. 1963).
longer at the site to accomplish a long overwater flight. If a direct overwater route is followed from Los Tuxtlas by any of our study species, two possible destinations are Galveston, Texas and Mobile, Alabama, which are each 1,150 km from the Sierra de Los Tuxtlas. Our calculations, based on Tucker (1974) and Nisbet et al. (1963), indicate that individuals of the study species varied in the distances they are capable of flying from the site. For no taxa did the average individual carry sufficient fuel reserves for a single trans-gulf flight (Tables 7, 8; Fig. 4). No greater proportion of the populations of trans-gulf migrants was capable of making such a flight than taxa with coastal or dual migration strategies (Table 8). This provides strong inference that birds were generally not crossing the Gulf of Mexico directly from the Isthmus of Tehuantepec on the night following their capture, and that this stopover site is used more for short-distance movements than as a staging site for long movements (Warnock 2010). These estimates assume calm wind conditions across the Gulf of Mexico. The proportion of individuals capable of the flight might increase substantially with a tail wind.

<table>
<thead>
<tr>
<th>Species</th>
<th># of individuals</th>
<th>% of population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empidonax spp.</td>
<td>NA 0</td>
<td>NA 0.0</td>
</tr>
<tr>
<td>Gray-cheeked Thrush</td>
<td>2 2</td>
<td>3.5 3.5</td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>35 18</td>
<td>11.0 5.7</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>3 3</td>
<td>2.6 2.6</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>0 0</td>
<td>0.0 0.0</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>2 1</td>
<td>5.1 2.6</td>
</tr>
<tr>
<td>Kentucky Warbler</td>
<td>12 7</td>
<td>9.0 5.3</td>
</tr>
<tr>
<td>Hooded Warbler*</td>
<td>23 0</td>
<td>13.5 0.0</td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>12 7</td>
<td>15.4 9.0</td>
</tr>
<tr>
<td>Yellow-breasted Chat</td>
<td>NA 0</td>
<td>NA 0.0</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>2 0</td>
<td>2.9 0.0</td>
</tr>
<tr>
<td>Painted Bunting</td>
<td>NA 0</td>
<td>NA 0.0</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>13 1</td>
<td>8.3 0.6</td>
</tr>
</tbody>
</table>

*The dramatic difference between the two methods may be a result of the substantial difference between the average fat-free masses of the two techniques in a relatively small species (1.32 g).
Winker (1995a) suggested the majority of captures at this site during autumn were not birds arriving from a trans-gulf flight, but were likely birds moving south along the coast to arrive in Los Tuxtlas. Birds from this same site in spring were likely reversing Winker's (1995a) proposed route and following the coast northward before perhaps making shorter overwater crossings of the northern Gulf or avoiding overwater flights altogether. Eleven of our 13 study taxa occurred in substantial numbers in Rappole et al.'s (1979) study of a stopover site in southern Texas in spring. This suggests some individuals of species thought to be exclusively trans-gulf migrants are moving northward along the Gulf Coast, perhaps crossing few areas or only short distances over open water. Another possibility is that trans-gulf migrants are moving eastward along the southern coast of the Gulf of Mexico and making the crossing by way of the Yucatan Peninsula. Both possibilities allow for arrival of migrants at observation points in the southeastern United States either by land or water (Stevenson 1957, Godthreux 1971, Rappole et al. 1979, Wang and Moore 1997). Sampling migrant abundance along the Gulf Coast from the Isthmus northward would provide valuable information about departure and arrival points for trans-gulf migrants.

Fueling Strategies.—Migration routes and distances to breeding areas failed to explain variation in mass gains among species either within or between seasons. Species-level comparisons for our distance estimates in breeding areas are complicated by two factors that we cannot address: the origins and destinations of captured individuals are unknown, and both will likely affect fattening strategies. However, most variation in our data may have a proximate explanation in the relationship found by Dunn (2001): that individuals arriving at a site with lower mass gain more than those arriving with more substantial reserves. Dunn (2001) proposed that individuals arriving at a stopover site with sufficient resources only need a place to rest and maintain reserves, and they may not have substantial net gains even in ideal habitat. The significant negative relationship we found (Fig. 3) between a species-level estimate of fat levels and the amount of fuel a species gained (on average) in a day at this site suggests this relationship may scale up to the species level and help explain single-site patterns among species. A second and perhaps not unlinked relationship that we found is that species that tend to spend more time on the site were also likely to show higher diel gains than those remaining only a few hours (Tables 3, 6). We found a significant positive correlation between the percent of recaptures occurring after 24 hrs (Table 6) and the slopes of the condition index gains. These two findings may provide better insight into interspecific patterns of refueling in Los Tuxtlas than routes, distances traveled, or even seasonality through a complete migration cycle.

Current hypotheses regarding migration through Middle America need refinement. Species thought to be exclusively trans-gulf migrants were, on average, carrying insufficient resources to accomplish a Gulf crossing from Los Tuxtlas and may often not make such crossings. Refueling rates at this site are not higher in spring, and considerable variation occurs among species and between seasons. The total amount of fat carried and time spent at the site appear to be the best predictors of diel refueling gains.

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MOLT PATTERNS, BIOMETRICS, AND AGE AND GENDER CLASSIFICATION OF LANDBIRDS ON SAIPAN, NORTHERN MARIANA ISLANDS

PAUL RADLEY,1,3 ANDREA L. CRARY,2 JAMES BRADLEY,2 CHRISTINA CARTER,2 AND PETER PYLE2

ABSTRACT.—Molt strategies and plumage development by age and gender are poorly understood for resident tropical landbirds. We used data from six banding stations on Saipan, Northern Mariana Islands, and examination of 267 museum specimens to describe patterns of molt and to establish criteria for assessing age and gender of nine native resident landbird species on the island. Feather replacement sequences in the majority of Saipan's resident landbirds were typical of related species. Preformative molts occurred in at least eight of the nine species; these and definitive prebasic molts were incomplete to complete, and prealternate molt appeared to be absent for all species. We developed criteria for classifying gender of sexually dimorphic species using plumage cues, presence of brood patch or cloacal protuberance, and biometrics. We confirmed whether or not both brood patch and cloacal protuberance were reliable indicators of gender during breeding in monomorphic species. Distinct periods or seasons of molt are not well defined and can vary between years. Age classification of first-cycle birds based on molt limits, feather shape and condition, and extent of skull pneumatization is possible for most landbird species sampled on Saipan.

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Data concerning molt and plumage development indicate most tropical resident landbird species undergo a single annual prebasic molt that generally follows or partially overlaps their breeding seasons, whereas prealternate molts appear to be rare (Prys-Jones 1982; Avery 1985; Pyle et al. 2004; Ryder and Wolfe 2009; Wolfe et al. 2009a, b). Most available data relate to species of the Neotropics, but six species in the Hawaiian Archipelago exhibit a similar trend in seasonal molt strategies (e.g., Banks and Laybourne 1977, Fancy et al. 1993, Jeffery et al. 1993, Pratt et al. 1994, Ralph and Fancy 1994, Simon 1998, VanderWerf 2001). However, comparable literature regarding molt for avian species on oceanic islands in other tropical regions of the Pacific is entirely lacking.

Understanding a population's demographic parameters is critical when developing and implementing species conservation and management strategies (Anders and Marshall 2005, VanderWerf 2008, Saracco et al. 2009). Accurate assignment of age and gender of captured individuals, both of which may be based upon molt strategies, plumage development, and reproductive status is necessary to estimate vital rates of avian species. Vital rates are presently unknown for landbird species on Saipan, an oceanic island in the Mariana Archipelago of the western tropical Pacific Ocean. The Commonwealth of the Northern Mariana Islands' Division of Fish and Wildlife (CNMI-DFW) began collaboration with the Institute for Bird Populations (IBP) in 2007 to initiate the Tropical Monitoring of Avian Productivity and Survivorship (TMAPS) project on the island.

We established six TMAPS banding stations on Saipan in spring 2008 to collect baseline population data for landbirds in several cover types. The ultimate intent of the TMAPS Project on Saipan is to accrue data necessary to guide pre-emptive avian conservation efforts on the island, which focus on several species potentially threatened with extinction or extirpation by potential introduction of the brown tree snake (Boiga irregularis). This introduced snake was responsible for extinction or extirpation of nine of 12 species of native forest landbirds on Guam within the last half-century (Savidge 1987, Rodda and Savidge 2007), and is thought to be the single greatest threat to terrestrial ecosystems in the Northern Mariana Islands (Colvin et al. 2005).

We present information on molt and establish criteria for assignment of age and gender based on plumage, skull condition, eye color, wing chord, breeding condition, and relevant morphometric data for nine resident species of landbirds common to Saipan and other islands in the near vicinity. We update preliminary information
based on specimen examination and initial banding data presented by Pyle et al. (2008).

METHODS

Saipan (15° 12’ N, 145° 45' E), a tropical Pacific island (122.9 km²) in the Mariana Archipelago, is characterized by a rugged north-south limestone ridge which reaches an elevation of 436 m with low lying plateaus extending from its base. The island’s major habitat cover types are native limestone evergreen forest, tangan-tangan (Leucaena leucocephala) scrub, mixed evergreen forests, tropical savannas, and swordgrass (Miscanthus floridulus) thickets. Saipan’s climate is marine tropical, hot and humid, and characterized by relatively high and uniform yearly temperatures. A wet season generally occurs from July through October, the last 2 months have increased incidence of typhoons.

CNMI-DFW and IBP established six banding stations on Saipan in 2008 to monitor productivity and survivorship of the island’s landbird populations. Stations were specifically placed to facilitate sampling birds in all representative cover types or some combination thereof. Each station comprised 8-1012-mm mist nets operated one morning during each of nine 10-day periods from 13 April to 17 July 2008 and 11 April to 15 July 2009. We captured 1,778 individuals of nine species of native resident landbirds 2,419 times over the two seasons. Standard measurements and morphometric data were collected for all birds captured; age and gender were assigned to each following criteria in Pyle (1997, 2008; and developed in this paper). We also operated the stations from 20 February to 15 October 2010 and collected additional data on molt, biometrics, and plumage patterns. Pyle reviewed 267 relevant museum specimens (range = 8-53/species) prior to the 2008 TMAPS season to establish preliminary criteria for age and gender classification (Pyle et al. 2008). Most specimens had been collected on Saipan but some were collected elsewhere in the Mariana Islands or Micronesia, provided they represented the same species and subspecies occurring on Saipan. The gender of most specimens examined had been previously established by gonadal examination; these specimens formed the basis for gender-specific measurement and plumage differences reported. Criteria for gender classification were further assessed based on presence or absence of reproductive characters (brood patch and cloacal protuberance) in birds captured during presumed periods of breeding for each species on Saipan.

Molt and plumage terminology is based upon Howell et al.’s (2003) revision of Humphrey and Parkes (1959) nomenclature, while feather-tract and age terminologies, flight-feather numbering, and other abbreviations follow Pyle (1997, 2008). Primaries and primary coverts are numbered from the innermost (primary 1) to outermost (primary 9 or 10), secondaries from the outermost (secondary 1) to innermost tertials (secondary 9, 10, or 11), and rectrices from the central pair (rectrix 1) to the outermost pair (rectrix 5 or 6). Abbreviations used include; PF = preformative (formerly considered ‘first prebasic’) molt, DPB = definitive prebasic molt, BP = brood patch, and CP = cloacal protuberance.

Accurate age classification may be complicated by an apparent lack of distinct, calendar-year breeding seasonality of birds on Saipan, a trait that can be exhibited by species resident in tropical latitudes (Wolfe et al. 2009a, b). Thus, age diagnostics and classifications follow the molt-cycle-based system devised by Wolf et al. (2010) for tropical species and include: FCJ, a bird in its first molt cycle and entirely in juvenal plumage; FCF, a bird in its first molt cycle and in formative plumage (or having begun the preformative molt); SCB, a bird in its second molt cycle (or having begun the second prebasic molt) and in basic plumage; TCB, a bird in its third molt cycle (or having begun the third prebasic molt) and in basic plumage; and DCB, a bird in its definitive molt cycle (or having begun the definitive prebasic molt) and in basic plumage.

We report our findings of molt and classification of age and gender for nine of 14 native landbirds resident to Saipan, four of which are endemic to the Mariana Archipelago. Sample sizes for each species indicate the number of specimens examined, the number of individuals captured and processed, and the total number of individual captures. We report feather-replacement sequence as ‘typical’ if it proceeded distally from primaries 1 to 10, and proximally from secondaries after the tertials had been replaced (cf. Pyle 1997); the two doves showed an extra center at secondary 5 as is typical in diastatixic birds (Pyle 2008). We did not detect evidence of prealternate molts in any species.

RESULTS

White-throated Ground Dove (Gallicolumba xanthonura; n = 21 specimens, 38 individuals, 43 captures). Both PF and DPB are incomplete to
TABLE 1. Select biometrics useful for gender classification for nine species captured on Saipan, 2008–2009, including 267 museum specimens examined prior to initial field work in 2008. Mass of Mariana Fruit Dove and female Nightingale Reed Warbler was excluded because of small sample sizes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Measurement</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-throated Ground Dove</td>
<td>Wing chord (mm)</td>
<td>142.3 ± 6.0 (26)</td>
<td>132.8 ± 4.2 (26)</td>
</tr>
<tr>
<td>Mariana Fruit Dove</td>
<td>Mass (g)</td>
<td>114.4 ± 13.8 (15)</td>
<td>100.3 ± 10.4 (18)</td>
</tr>
<tr>
<td>Collared Kingfisher</td>
<td>Wing chord (mm)</td>
<td>127.9 ± 2.9 (18)</td>
<td>123.3 ± 2.9 (14)</td>
</tr>
<tr>
<td>Micronesian Myzomela</td>
<td>Mass (g)</td>
<td>113.6 ± 3.1 (24)</td>
<td>116.2 ± 3.2 (29)</td>
</tr>
<tr>
<td>Rufous Fantail</td>
<td>Wing chord (mm)</td>
<td>79.3 ± 5.4 (16)</td>
<td>84.3 ± 5.6 (19)</td>
</tr>
<tr>
<td>Nightingale Reed Warbler</td>
<td>Mass (g)</td>
<td>114.4 ± 1.5 (56)</td>
<td>118.5 ± 1.5 (37)</td>
</tr>
<tr>
<td>Bridled White-eye</td>
<td>Wing chord (mm)</td>
<td>71.8 ± 2.9 (72)</td>
<td>64.9 ± 1.9 (45)</td>
</tr>
<tr>
<td>Golden White-eye</td>
<td>Mass (g)</td>
<td>67.3 ± 1.6 (67)</td>
<td>65.0 ± 1.5 (94)</td>
</tr>
<tr>
<td>Micronesian Starling</td>
<td>Wing chord (mm)</td>
<td>87.6 ± 2.2 (9)</td>
<td>82.0 ± 2.9 (4)</td>
</tr>
</tbody>
</table>

Mean ± SD (n) | Range | Mean ± SD (n) | Range

- White-throated Ground Dove: 130-152, 126-141
- Mariana Fruit Dove: 100.9-139.7, 78.5-126.1
- Collared Kingfisher: 108-118, 110-125
- Micronesian Myzomela: 66.4-86.1, 75.4-94.8
- Nightingale Reed Warbler: 62-70, 60-69
- Bridled White-eye: 48-61, 45-55
- Golden White-eye: 64-83, 60-69
- Micronesian Starling: 71-9.0, 68.5-95

Plumage maturation rates is needed. Both males and females may have BPs and biometrics may be helpful with ascertaining gender (Table 1).

Mariana Fruit Dove (*Ptilinopus roseicupillo*: n = 33 specimens, four individuals, four captures). Both PF and DPB are incomplete to complete. Most apparent limits in the primaries or secondaries may be due to protracted or suspended molt, but retention of one to three secondaries (of 10 total) during incomplete molt also occurs, most often among secondaries 7 and 8. Juvenile primary 10 is thick, rounded, and dull brown in juveniles (FCJ) and moltling FCJ birds, and the juvenile rectrices and secondaries are narrow. Primary 10 in DCB and complete FCF birds is thinner and more pointed, and the rectrices and secondaries are broader. Older DCB birds (at least TCB) can show mixed generations of definitive secondaries. FCF and DCB males have more extensive magenta on the crown, a bluish-tinge on the nape, and a broader yellow tail band whereas FCF and DCB females have less magenta in the crown, little to no bluish-coloring on the nape, and a faint yellow tail band. Both males and females may have BPs and biometrics appear to be of limited use for assigning gender (Table 1).

Collared Kingfisher (*Todiramphus chloris*: n = 17 specimens, 72 individuals, 91 captures). PF is incomplete. One to three secondaries between secondaries 1 and 7 (of 11 total) can be retained during both PF and DPB. FCF birds often exhibit limits between formative and juvenile secondaries and, at times, within the greater coverts. Older birds often have one generation of feathers but can show retained juvenile (in SCB birds) or definitive (in TCB or older birds) secondaries, often among secondaries 4 and 5. Juvenile females are brown with a broad cinnamon tail band and broad rufous to cinnamon edging on the primary and secondary coverts. DCB females are similar to juveniles in appearance but have narrower and paler edging on the primary and secondary coverts. Juvenile males are similar to juvenile females but lack a cinnamon tail band. FCF males are distinctive and have variable amounts of gray on the head and nape, and white on the throat and breast. The grayish-brown juvenile body plumage is largely retained and motled with purple formative feathers on the back. DCB males have brown body plumage with purplish and copper iridescence on the back and wings, and varying amounts of white on the head, throat, and upper breast. The amount of white plumage in males may be age-dependent with more brown or gray motting in younger (e.g., SCB and TCB) birds and less in older birds, but confirmation of
absent and the DPB is complete and proceeds in typical sequence. Juveniles exhibit white scalloping on the secondary coverts and light gray scalloping on the breast. The covert scalloping is more reliable for assigning age of worn birds than the breast scalloping, which can wear off. The blue or turquoise color on the inner vane of the flight feathers is reduced in juveniles, whereas in adults the coloring extends almost to the edge of the feather on both the inner and outer vanes. Female plumages exhibit a reddish-brown backs and turquoise-green wings, tail, and eye-stripe, whereas males have turquoise backs and bright blue wings, tail, and eye-stripe. These plumage traits occur in all age classes but colors average brighter in DCB than in FCF individuals. Juvenile outer primaries are narrow and tapered, whereas basic primaries are broader but are, on average, narrower for females than for males. Females exhibit BPs, which may also occur for males. It is not known whether CPs occur in males. Biometrics suggest slight reverse sexual size dimorphism and appear to be of limited use for assigning gender (Table 1).

Micronesian Myzomela (Myzomela rubra; n = 32 specimens, 121 individuals, 142 captures). The PF is incomplete to complete and includes body feathers, secondary coverts, and some to all primaries, secondaries, primary coverts, and rectrices in typical sequence. The DPB is complete but can be protracted and/or suspended. Juveniles (FCJ) often exhibit fleshy yellow gapes and have not yet initiated molt. Contrasts are often observed between inner primaries and outer secondaries due to protracted and/or suspended molt and normal fading and wear. FCF individuals often retain blocks of middle secondaries, and, less often, outer primaries and primary coverts, which are more tapered, worn, and faded than replaced feathers. FCF females have brown formative flight feathers and mottled brown and red body plumage, whereas FCF males have dark brown formative flight feathers and red body plumage mottled brown. DCB birds have one feather generation, although a gradient of fading and wearing is often evident within the primaries and secondaries. DCB females can be quite red with brown mottling and medium brown wings while DCB males are bright red with black wings. Plumage is useful for assigning age and gender, whereas biometrics appear to be of little help with the latter (Table 1). The extent of skull pneumatization is difficult to ascertain because of the species’ dark, non-transparent skin. BPs and CPs are reliable for classification of males and females during breeding periods.

Rufous Fantail (Rhipidura rufifrons; n = 41 specimens, 821 individuals, 1,299 captures). The PF is usually partial and includes some body feathers, some to all (range = 2–9) greater coverts and, at times, the carpal covert. Some individuals undergoing a complete molt in September–October 2010 appeared to be young and were possibly undergoing a complete PF but may also have been hatched in late winter and undergoing a second prebasic molt after a PF in the spring. The DPB is complete but can be protracted and/or suspended. Molt can be in typical sequence or occasionally primaries can commence replacement within the tract and proceed both proximally and distally. Juvenile greater coverts, and occasionally carpal covert and alula, are brown with distinct rufous-buff tips and edging that fade with age, whereas basic coverts are uniformly brown with or without thin rufous edging. FCF in both males and females shows molt limits within the greater coverts, between the outer greater coverts and the carpal covert, or occasionally between the carpal covert and the alula. Neither males nor females show suspension limits or molt clines in the primaries, as can be shown by DCB individuals. Juvenile flight feathers and primary coverts on FCF birds are duller brown and more tapered than basic feathers on DCB birds. Extent of skull pneumatization can be useful for assigning age classes. Juveniles exhibit large skull windows that slowly pneumatize resulting in small windows being visible in some FCF individuals post-PF; skulls in all DCB individuals are completely pneumatized. Males and females are similar in both plumage and biometrics (Table 1), but both CPs and BPs are reliable for assigning gender of breeding birds.

Nightingale Reed Warbler (Acrocephalus luscintius; n = 8 specimens, 14 individuals, 17 captures). Both PF and DPB are complete and appear to proceed in typical sequence. FCJ and DCB are similar, but juvenile primaries and secondaries are slightly more rounded and rectrices are thinner and more tapered than basic rectrices. Skulling can be reliable for separating FCJ and FCF birds but timing of reliability needs to be examined. Sample sizes are small, but wing chord may be useful for assigning gender; some overlap likely occurs (Table 1). BPs and CPs are useful for assigning gender of breeding individuals.
Bridled White-eye (*Zosterops conspicillatus*; *n* = 53 specimens, 360 individuals, 389 captures). The PF is complete to incomplete and DPB is complete. Feather-replacement sequence among primaries (at least) appears to be irregular. Incomplete PF includes all body feathers, all wing coverts, and most flight feathers, with some FCF individuals retaining small blocks of juvenile secondaries. The DPB occurs primarily post-breeding, but potentially can occur before or during the breeding season. FCF and DCB of both males and females are similar in size and plumage following the PF, but FCF can often be identified by extent of skull pneumatization (timing of reliability needs to be examined). Males and females are similar in plumage and metrics (Table 1; the apparent dimorphism in mass is likely an artifact of assigning gender by breeding condition only; i.e., heavier females were gravid) but CP and BP are reliable for assigning gender during breeding seasons.

Golden White-eye (*Cleptornis marchei*; *n* = 16 specimens, 324 individuals, 410 captures). The PF is partial and the DPB is complete; the feather-replacement sequence may or may not be irregular as in Bridled White-eye. The PF includes body feathers and possibly some lesser, median, and inner greater coverts on some birds. Replaced feathers are darker and more yellowish-green than retained greenish-brown juvenile feathers, the latter becoming increasingly faded and worn as the plumage ages. DCB birds have yellow heads, orange bills, and yellowish-green wing and back plumage. Juveniles have white molting and paler yellow feathers on the head and face prior to the PF, and often have largely unpneumatized skulls. Very young juveniles exhibit dusky coloring at the base of the bill and, at times, on the tarsi. Some FCF birds also have partially unpneumatized skulls, but timing of reliability in relation to PF needs to be examined. Length of wing chord, exposed culmen, and nares in tip of bill are useful for assigning gender (Table 1). BPs and CPs are reliable for assigning gender during breeding, although some males can develop partial BPs.

Micronesian Starling (*Aplonis opaccir*, *n* = 46 specimens, 24 individuals, 24 captures). The PF is partial and the DPB is complete and proceeds in typical sequence. The PF includes body feathers and some lesser and median coverts. Juveniles (FCJ) and FCF are dark with lighter-streaked breast and belly feathers. DCB individuals are glossy black with males being glossier than females. Wing chord and CP/BP (during breeding) are reliable for assigning gender (Table 1).

**DISCUSSION**

We provide previously unknown information on molt patterns and age and gender delineation for nine species of resident landbirds that commonly occur on Saipan. Our data indicate that molt strategies of most birds captured on the island are like those of resident landbirds in other tropical locations (Banks and Laybourne 1977; Prys-Jones 1982; Avery 1985; Fancy et al. 1993; Jeffery et al. 1993; Pratt et al. 1994; Ralph and Fancy 1994; Simon et al. 1998; VanderWerf 2001; Pyle et al. 2004; Ryder and Wolfe 2009; Wolfe et al. 2009a, b) and in North American temperate locations (Pyle 1997, Howell et al. 2003). Preformative molt occurred in all species except Collared Kingfisher, while definitive prebasic molt was incomplete to complete across all nine species and prealternate molt appeared to be absent.

Separation of birds in juvénal, formative, and definitive plumages was possible for all nine landbird species captured on Saipan, based upon plumage patterns, molt limits, feather shape and condition, and extent of skull pneumatization; some individuals of the two dove species can be identified in third-basic or later plumages. Accurately classifying age of resident birds on Saipan, similar to resident species in most other tropical locations (e.g., Wolfe et al. 2009a, b), can be challenging because of a lack of distinct seasonality in breeding and the difference in breeding season duration when compared to their temperate counterparts. Breeding and molt were observed to overlap in at least one species (i.e., Bridled White-eye) and timing of molt and breeding between 2008 and 2009 was not consistent. Some species on Saipan are known to breed more than once in a calendar-year or to be capable of breeding year-round (e.g., Craig 1996, Mosher and Fancy 2002). The temperate calendar-based age classification system could not properly be used to classify age of birds captured on Saipan. Likewise, the months in which age classes could be reliably ascertained (i.e., ‘age brackets’; Wolfe et al. 2010) for each species cannot yet accurately be estimated. We need more data to establish age brackets for each species, which will be used in combination with calendar-based age codes and information on molt strategies and breeding seasons, to most accurately reflect age of individuals and age structure within populations.
Criteria presented to discriminate age class and gender serve as a baseline for assessing vital rates of the majority of avian species on Saipan. This improves our ability to guide targeted conservation strategies, including species conservation introductions or translocations (IUCN 1987, 1998) to establish self-sustaining, satellite populations on islands in the Mariana Archipelago safe from the brown tree snake. DFW currently executes conservation measures for avian species in the Marianas with little or no baseline natural history information to guide decision making. The ability to accurately identify gender of individuals will help ensure even sex ratios during translocation, increasing the long-term success of such efforts. Knowledge of which cover types promote the best overall survival, productivity, and recruitment in landbird populations on Saipan should enable us to better match species with suitable islands and increase the likelihood of success of translocation strategies in the Northern Marianas Islands.

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LITERATURE CITED


PARROT BEHAVIOR AT A PERUVIAN CLAY LICK
DONALD J. BRIGHTSMITH1,3 AND ETHEL M. VILLALOBOS2

ABSTRACT—We documented the behavior of 13 parrot species at a geophagy site along the Tambopata River in southeastern Peru. These species use the lick in one or more multi-species aggregations composed predominantly of (1) large parrots and small macaws (81% of lick use), (2) large macaws (5%), or (3) parakeets and small parrots (5%). Monospecific flocks accounted for only 8% of lick use and lone individuals < 1% of lick use. The multi-species aggregations sorted by body size and were generally composed of species with similar coloration suggesting that group composition was driven by a mix of competition and predation. Three species regularly used the lick in monospecific groups and these had the largest group sizes away from the lick, suggesting a causal relationship between intraspecific sociality and lick use in monospecific groups. All groups were wary when approaching the lick, probably due to the risk from landslides and predators. We suggest that clay lick use strategies are molded by predation risk and competition acting on a suite of species with varying body size, coloration, and gregariousness. Received 12 July 2009. Accepted 1 March 2011.

Geophagy, the intentional consumption of soil, has been documented for a wide range of mostly herbivorous mammals, reptiles, and birds (Sokol 1971, Klaus and Schmid 1998, Diamond et al. 1999, Brightsmith 2004). Hundreds of birds (up to 17 species) gather daily at river-edge ‘clay licks’ to consume soil throughout the western Amazon Basin (Emmons and Stark 1979, Burger and Gochfeld 2003, Brightsmith 2004). The birds, mostly psittacines, apparently consume soil for its high concentration of sodium (Brightsmith and Aramburú 2004, Brightsmith et al. 2008), but may also receive protection from dietary toxins (Gilardi et al. 1999). Aggregations of birds which use clay licks vary greatly in species composition and patterns of lick use, and much of this variation remains unexplained (Burger and Gochfeld 2003, Brightsmith 2004, Brightsmith and Aramburú 2004, Lee et al. 2009).

Observations suggest the birds’ behavior at clay licks has been molded by predation and competition, but few detailed studies have been conducted (Burger and Gochfeld 2003, Brightsmith 2004, Brightsmith and Aramburú 2004). Social forces such as information exchange, search for mates, and parental care favor group formation (Ward and Zahavi 1973, Wright et al. 2003). However, there are many costs to group membership including competition for resources (Grand and Dill 1999, Krause and Ruxton 2002) and disease transmission (Hoare et al. 2000). Clay licks and other geophagy sites provide good opportunities to study mixed species aggregations. We studied the behavior of parrots using a large clay lick along the upper Tambopata River in southeastern Peru in an effort to document lick use strategies for comparison with research at other sites in the region (Burger and Gochfeld 2003).

METHODS

Study Area.—Tambopata Research Center (13° 08' S, 69° 36' W) is in the Department of Madre de Dios in southeastern Peru in the Tambopata National Reserve (275,000 ha) near Bahuaja-Sonene National Park (1,091,000 ha). The area is tropical moist forest near the boundary with subtropical wet forest. The elevation is 250 m asl with 3,200 mm of rain per year and a wet season from October to March (Tosi 1960, Brightsmith 2004). The area contains a mix of mature floodplain forest, successional floodplain forest, Mauritia flexuosa palm swamps, and upland forest (Foster et al. 1994).

The clay lick studied was a 500-m long, 25–30 m high, cliff on the right bank (west side) of the upper Tambopata River. The lick was apparently formed by the river’s erosion of recently uplifted Tertiary age alluvial sediments (Räsänen and Salo 1990, Foster et al. 1994, Räsänen and Linna 1998). It consists of two large exposed areas ~150 m in length on the south end and 200 m in length on the north end. The two are separated by a landslide of ~150 m in width. The south end contains a clay layer ~15–17 m high, topped by a band of sand and cobble about 5 m thick. The north end has clay about 8 m high topped by 8 m of sand and cobble. The soils of the clay layer are rich in high cation exchange capacity clays with high sodium levels.
TABLE 1. Sociality of parrot species on the clay lick at Tambopata Research Center, Peru during 20 mornings from December 2002 to January 2003. The species are arranged by body mass. 'Green macaws' were recorded when observers could not distinguish between Chestnut-fronted and Red-bellied Macaws. Monospecific = percent of counts for which the species was recorded on the lick in a monospecific group. Large Parrot = percent of counts when the species was part of the large parrot aggregation. Parakeet and Large Macaw = percent of counts for which species were part of the parakeet and large macaw aggregations. Total = number of bird minutes recorded for the species. Body masses are from Dunntn et al. (1991) and Terborgh et al. (1990).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>Large parrot</th>
<th>Large macaw</th>
<th>Parakeet</th>
<th>Mono-specific</th>
<th>Other</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-and-green Macaw</td>
<td>1,250</td>
<td>40</td>
<td>52</td>
<td>2</td>
<td>7</td>
<td>0</td>
<td>124</td>
</tr>
<tr>
<td>Blue-and-yellow Macaw</td>
<td>1,125</td>
<td>49</td>
<td>45</td>
<td>1</td>
<td>6</td>
<td>0</td>
<td>1,137</td>
</tr>
<tr>
<td>Scarlet Macaw</td>
<td>1,015</td>
<td>56</td>
<td>42</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>574</td>
</tr>
<tr>
<td>Mealy Amazon</td>
<td>610</td>
<td>96</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>12,471</td>
</tr>
<tr>
<td>Yellow-crowned Amazon</td>
<td>510</td>
<td>79</td>
<td>3</td>
<td>2</td>
<td>9</td>
<td>6</td>
<td>130</td>
</tr>
<tr>
<td>Chestnut-fronted Macaw</td>
<td>430</td>
<td>95</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2,267</td>
</tr>
<tr>
<td>'Green Macaw'</td>
<td>100</td>
<td></td>
<td>0</td>
<td>0</td>
<td></td>
<td>0</td>
<td>336</td>
</tr>
<tr>
<td>Red-bellied Macaw</td>
<td>370</td>
<td>96</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>1076</td>
</tr>
<tr>
<td>Blue-headed Macaw</td>
<td>250</td>
<td>72</td>
<td>0</td>
<td>28</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Blue-headed Parrot</td>
<td>247</td>
<td>83</td>
<td>13</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1,210</td>
</tr>
<tr>
<td>White-eyed Parakeet</td>
<td>157</td>
<td>68</td>
<td>5</td>
<td>8</td>
<td>17</td>
<td>2</td>
<td>11,363</td>
</tr>
<tr>
<td>White-bellied Parrot</td>
<td>155</td>
<td>0</td>
<td>43</td>
<td>58</td>
<td>0</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Orange-cheeked Parrot</td>
<td>140</td>
<td>69</td>
<td>1</td>
<td>22</td>
<td>1</td>
<td>7</td>
<td>259</td>
</tr>
<tr>
<td>Dusky-headed Parakeet</td>
<td>108</td>
<td>1</td>
<td>0</td>
<td>92</td>
<td>7</td>
<td>0</td>
<td>537</td>
</tr>
<tr>
<td>Totals (bird minutes)</td>
<td>25,400</td>
<td>1,727</td>
<td>1,555</td>
<td>2,580</td>
<td>280</td>
<td>31,542</td>
<td></td>
</tr>
</tbody>
</table>

(Gilardi et al. 1999, Brightsmith et al. 2008). The slope of the lick face ranges from moderate (~30°) to nearly vertical (80°).

**Lick Counts.**—Data were collected during December 2001 and 2002, and January 2000 and 2003 from a point ~200 m from the clay lick. Observers arrived before sunrise and stayed until the end of the early morning activity (0700 to 0730 hrs). Observers watched the staging birds and recorded when the first group of birds began to fly in slow circles in front of the lick in anticipation of landing. Observers counted all birds perched on each section of the clay lick every 5 min (Brightsmith 2004). More detailed location data were collected in December 2002 and January 2003 (n = 20 mornings) for each bird on the lick to quantify the social group membership of each species using the lick.

**Arrivals and Disturbance.**—Observers recorded the numbers and species of parrots as they arrived in the area from a point on the opposite river bank ~400 m to the east of the clay lick. It was not possible to record the birds that arrived from forests behind the lick (to the west).

Observers recorded the cause of the disturbance whenever >25% of the birds simultaneously flew from the clay lick or surrounding trees.

**Data Analyses.**—The clay lick use by each species was calculated as the total number of 'bird minutes' on the lick (Brightsmith 2004). Bird minutes were defined as the number of birds on the lick multiplied by the number of minutes they stayed on the lick (i.e., 4 birds for 15 min each = 60 bird min). We conducted principal component analysis of the data for birds which simultaneously shared each section of the lick to identify the groups of species which used the lick together. Only principal components with eigenvalues ≥1 are reported. We tested differences among species for group sizes arriving at the lick using Kruskal-Wallace and Mood’s median test with 95% confidence intervals around the medians using StatGraphics Centurion XV. Normal variables are presented as mean ± SD, while those that failed Shapiro-Wilks’ test for normality are presented as medians with 95% confidence intervals. Alpha = 0.05 for all statistical tests.

**RESULTS**

Thirteen species of psittacines used the clay lick in the early morning period (before 0730 hrs; Table 1). Over 99% of all lick use was in groups. Mixed species aggregations accounted for 92% of the total lick use, monospecific groups 8%, and single individuals <1% (Table 1).

Five principal components (eigenvalue > 1) together explained 58% of the variance in group composition on the clay lick (Table 2). These
TABLE 2. Weights for the five principal components which explain the most variance in group composition of psittacines at an avian geophagy site in southeastern Peru. All principal components have eigenvalues >1. Each principal component is identified with a text label which describes the bird aggregation it represents. The most abundant species in each aggregation are shown in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>PC I</th>
<th>PC II</th>
<th>PC III</th>
<th>PC IV</th>
<th>PC V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-and-green Macaw</td>
<td>0.09</td>
<td>0.56</td>
<td>-0.03</td>
<td>0.09</td>
<td>0.12</td>
</tr>
<tr>
<td>Blue-and-yellow Macaw</td>
<td>0.18</td>
<td>0.47</td>
<td>0.04</td>
<td>-0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>Scarlet Macaw</td>
<td>0.17</td>
<td>0.54</td>
<td>0.11</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>Chestnut-fronted Macaw</td>
<td>0.55</td>
<td>-0.09</td>
<td>-0.08</td>
<td>0.16</td>
<td>0.12</td>
</tr>
<tr>
<td>Red-bellied Macaw</td>
<td>0.45</td>
<td>-0.15</td>
<td>-0.08</td>
<td>0.22</td>
<td>0.21</td>
</tr>
<tr>
<td>Mealy Amazon</td>
<td>0.51</td>
<td>-0.20</td>
<td>-0.04</td>
<td>0.10</td>
<td>-0.05</td>
</tr>
<tr>
<td>Yellow-crowned Amazon</td>
<td>0.15</td>
<td>-0.13</td>
<td>0.17</td>
<td>-0.14</td>
<td>-0.69</td>
</tr>
<tr>
<td>Blue-headed Parrot</td>
<td>0.21</td>
<td>0.13</td>
<td>0.53</td>
<td>-0.14</td>
<td>-0.34</td>
</tr>
<tr>
<td>Orange-cheeked Parrot</td>
<td>-0.03</td>
<td>-0.12</td>
<td>0.66</td>
<td>-0.15</td>
<td>0.31</td>
</tr>
<tr>
<td>White-eyed Parakeet</td>
<td>0.23</td>
<td>-0.22</td>
<td>0.08</td>
<td>-0.27</td>
<td>0.21</td>
</tr>
<tr>
<td>Dusky-headed Parakeet</td>
<td>-0.15</td>
<td>-0.10</td>
<td>0.42</td>
<td>0.43</td>
<td>0.31</td>
</tr>
<tr>
<td>White-bellied Parrot</td>
<td>-0.16</td>
<td>0.02</td>
<td>0.49</td>
<td>0.22</td>
<td>0.31</td>
</tr>
<tr>
<td>Blue-eyed Macaw</td>
<td>-0.01</td>
<td>0.16</td>
<td>0.59</td>
<td>0.22</td>
<td>0.31</td>
</tr>
<tr>
<td>Percent variance explained</td>
<td>18</td>
<td>14</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
</tbody>
</table>

Principal components represent three mixed species aggregations which use the lick as distinct entities. The large parrot aggregation was composed of three abundant species: Chestnut-fronted Macaws (Ara severus), Mealy Amazons (Amazona farinosa), and Red-bellied Macaws (Orthopsittaca manilata). These were regularly joined by up to seven additional species: White-eyed Parakeet (Aratinga leucophthalma), Yellow-crowned Amazon (Amazona ochrocephala), Blue-headed Parrot (Pionus menstruus), Blue-and-yellow Macaw (Ara araruna), Scarlet Macaw (A. maccac), Red-and-green Macaw (A. chloropterus), and Orange-cheeked Parrot (Pyrilia barrabandi). This aggregation, represented by PC I, accounts for 18% of the variance in lick use. The large macaw aggregations contained three common species: Red-and-green Macaws, Scarlet Macaws, and Blue-and-yellow Macaws (PC II, 14% of the variance) which were rarely joined by Blue-headed Parrots, Mealy Amazons, White-eyed Parakeets, and Chestnut-fronted Macaws. The principal components analysis identified three parakeet and small parrot aggregations, one with Dusky-headed parakeets (Aratinga weddellii), Orange-cheeked Parrots, and Blue-headed Parrots (PC III, 9% of the variance), one with White-bellied Parrots (Pionites leucogaster), Blue-headed Macaws (Primolius couloni), and Dusky-headed Parakeets (PC IV, 9% of the variance), and one with Dusky-headed Parakeets, Orange-cheeked Parrots, and White-eyed Parakeets (PC V, 8% of the variance). These three groups were functionally similar: both formed around flocks of Dusky-headed Parakeets or occasionally White-eyed Parakeets and used the same part of the lick. Thus, these groups were considered collectively as the “parakeet aggregation”.

Ten species were recorded using the lick in monospecific groups, but most were monospecific remnants of the mixed species aggregations. Only three species regularly used the lick in coherent monospecific groups: White-eyed Parakeets, Dusky-headed Parakeets, and White-bellied Parrots (Table 2). Single psittacines were recorded on the lick 58 times and these birds were often leading larger groups of birds to the lick (36%) or remained when larger groups abandoned the lick (31%) leaving only 19 instances of single birds using the lick.

We focused on the three mixed-species aggregations as they accounted for >90% of the clay lick use. The three mixed-species aggregations were independent, as they arrived, staged, and descended to the lick separately, and used different areas of the lick. They also rarely reacted to each other’s alarm calls. The behavior of the birds at clay licks can be divided into three distinct phases: arrival in the area, descent to the lick, and lick use.

**Arrival in the Area.**—All birds arrived in monospecific flocks. Multiple species, when seen together, did not perch or stage together indicating they were just casual associations. Observers...
could not usually detect arrivals of White-bellied Parrots or Orange-cheeked Parrots as they flew lower than other species and arrived quietly. However, all other species regularly arrived flying high above the canopy and were readily detected.

The members of the large parrot aggregation began to arrive 8.4 ± 5.8 min before sunrise (n = 70 mornings) and usually perched in trees immediately above and behind the clay lick. The median arriving group size was two except for Red-bellied Macaws which was three (Table 3).

The first large macaws began arriving at about the same time as members of the large parrot aggregation (9.3 ± 11.7 min before sunrise, n = 70 mornings). The large macaws continued to arrive throughout the morning at a slow steady rate (1.1 ± 0.3 individuals/min, n = 577 birds over 6 days). Macaws arrived in pairs (61%), singles (30%), and rarely groups of three or four (7%, n = 291 groups; Table 3).

The members of the parakeet aggregation began to arrive 21.7 ± 15.6 min after sunrise (n = 68 mornings) and staged in short trees at the lick’s left edge. Both common parakeets arrived in large groups: Dusky-headed Parakeet median = 10, n = 34 groups, White-eyed Parakeet median = 22, n = 65 (Table 3). The arriving groups of parakeets were relatively large, but waited and joined with other conspecifics before moving to the lick.

Our observations suggest many birds spend hours socializing in the trees around clay licks without descending to eat soil. We focus in this paper on birds that consumed soil and do not address the social aspects of gathering near clay licks.

Descent to the Lick.—Most species were able to join more than one type of aggregation, but the three aggregations commonly approached the lick independently and in stereotypical patterns. The members of the large parrot aggregation began to move towards the clay lick by 15.7 ± 11.5 min (n = 66 mornings) after sunrise. There were at least 424 ± 152 birds in the area (n = 6 mornings) at this time. One or more small groups of birds (usually < 20) led the descent by flying in large circles in front of the lick. Birds from the trees joined these groups until there were up to 100 birds in flight. These flights lasted 3.4 ± 4.3 min (n = 62 mornings). The birds flew in slow circles in front of the lick, apparently choosing where to land. Detections of predators or landslides during these flights often caused the birds to choose an alternative section of the lick or break off approach completely.

The large macaw aggregations often formed as groups of 6–29 birds flew to the lick to join the tail end of the large parrot aggregation (96% of 69 mornings). Groups of up to 30 large macaws also initiated lick use on unoccupied sections of the clay lick (29% of 69 mornings). The latter occurred ~50 ± 23 min after sunrise (n = 26 mornings) when they staged and flew to the lick in a manner similar to that described for the large parrot aggregation.

Members of the parakeet aggregation descended to the left edge of the lick starting ~101 ± 21 min (n = 34 mornings) after sunrise. These groups did not engage in exploratory flights like the large parrot aggregation or large macaw aggregation, and instead moved deliberately through the trees progressively closer to the lick and then flew directly from the trees to the lick (usually a distance of <20 m). There were at least 217 ± 120 parakeets in the area (n = 5 mornings) by the time the first parakeet flocks descended to the lick.

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**TABLE 3.** Group size for arriving birds at the Tambopata Research Center clay lick based on six mornings of observations. Birds were not detected arriving in mixed species groups. Species which share superscript letters do not differ (Mood's median test, P > 0.05) in median group size.

<table>
<thead>
<tr>
<th>Species</th>
<th>Median Group Size</th>
<th>95% CI</th>
<th>Lower</th>
<th>Upper</th>
<th>1</th>
<th>2</th>
<th>3 or 4</th>
<th>≥5</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-and-green Macaw</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>36</td>
<td>64</td>
<td>0</td>
<td>0</td>
<td>22</td>
<td>0.005</td>
</tr>
<tr>
<td>Scarlet Macaw</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>34</td>
<td>57</td>
<td>9</td>
<td>0</td>
<td>127</td>
<td>0.008</td>
</tr>
<tr>
<td>Chestnut-fronted Macaw</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>31</td>
<td>54</td>
<td>11</td>
<td>4</td>
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<tr>
<td>Blue-and-yellow Macaw</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>21</td>
<td>62</td>
<td>13</td>
<td>4</td>
<td>142</td>
<td>0.261</td>
</tr>
<tr>
<td>Mealy Amazon</td>
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<td>46</td>
<td>21</td>
<td>8</td>
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<td>0.650</td>
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<td>Blue-headed Parrot</td>
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<td>2</td>
<td>3</td>
<td>22</td>
<td>29</td>
<td>29</td>
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<td>Red-bellied Parrot</td>
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<td>4</td>
<td>8</td>
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<td>27</td>
<td>51</td>
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</tr>
<tr>
<td>Dusky-headed Parrot</td>
<td>10</td>
<td>6</td>
<td>14</td>
<td>2</td>
<td>9</td>
<td>3</td>
<td>86</td>
<td>65</td>
<td>0.001</td>
</tr>
<tr>
<td>White-eyed Parakeet</td>
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<td>12</td>
<td>28</td>
<td>2</td>
<td>9</td>
<td>3</td>
<td>86</td>
<td>65</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Lick Aggregation Dynamics.—Groups of birds on the lick were fluid; large numbers of birds flew regularly between the surface of the clay lick and the adjacent trees. Some birds took pieces of clay and carried them to the trees for consumption. Thus, the maximum number of birds on the lick at any one time was substantially less than the total number of birds in the area. Entire feeding aggregations often abandoned the lick in response to alarm calls. No apparent cause for the alarm (n = 1,060 disturbances) was detected in 90% of cases and the birds usually returned to the lick almost immediately. Documented causes of disturbance were rockslides (4%), raptors (2%), other large birds (2%), and people or boats (1%).

The large parrot aggregations formed on 97% of mornings (n = 71) and accounted for 80% of the total lick use. Additional birds flew directly to the lick once the first birds landed, and numbers on the lick increased rapidly (152 ± 85.2 individuals on the lick 10 min after start, n = 65 mornings). Birds continued to arrive in the area and perch in the trees even after the first birds began to use the lick. At least 951 ± 262 birds (range = 791-1,428, n = 6 mornings) arrived per morning of which 92% were species that joined the large parrot aggregation (874 ± 260 birds, range = 621-1,336, n = 6 mornings). The daily maximum number of birds simultaneously on the lick in the large parrot aggregation averaged 192 ± 86 (range = 24 to 497, n = 69 mornings). The parakeet aggregation used the lick for 16.2 ± 11.4 min (n = 46 mornings).

The three large macaws used the lick in the early morning as part of the large parrot aggregation (50% of total early morning lick use) or in aggregations dominated by large macaws (49% of total early morning lick use, Table 1). The aggregations dominated by macaws formed on 46% of 71 mornings and accounted for 5% of the total lick use. The number of birds on the lick increased within the first 5 min (12 ± 9 at first detection, n = 28 mornings) and remained fairly stable thereafter (14 ± 7, n = 11, 10 min after first detection). The average maximum number of individuals was 17 ± 10 (n = 33 mornings). About 10% of the total birds that arrived in the vicinity of the lick were large macaws (96 ± 24 birds, range = 66-122, n = 6 mornings). The large macaw aggregations lasted 19 ± 13 min (n = 33 mornings).

The parakeet aggregations formed on 47% of 71 mornings and accounted for 5% of the total lick use. The majority of the birds in the parakeet aggregation were flocking parakeets and these flocks were restless, usually remaining on the lick for only a few minutes before taking flight and returning to the lick or adjacent trees. The average number of the birds on the lick, despite these fluctuations, remained fairly stable with time (27 ± 25 birds, n = 35 mornings, <5 min after descending to the lick vs. 23 ± 21 birds, n = 8 mornings, 10 min later). About 36% of all birds arriving at the lick were species that joined the parakeet aggregation (340 ± 240 birds, range = 95-653, n = 6 mornings). The maximum number of birds on the lick in parakeet aggregations averaged 40 ± 26 (range = 3 to 138, n = 34 mornings). The parakeet aggregation used the lick for 16.2 ± 11.4 min (n = 34 mornings) before they dispersed.

Spatial Distribution.—The clay lick was >1 km in length. However, 85% of the total clay lick use occurred on only four small areas, totaling only 18% of the exposed cliff. Each aggregation regularly used the same few lick areas. The large parrot aggregation used two sections with exposed clay 9.8 to 15.2 m and 1.4 to 8.3 m above the cliff base. Neither section had vegetation immediately adjacent to the area used by the birds. The large macaw aggregation used two tall center sections of the lick with exposed clay 7.8 to 15.7 m high. Both were isolated from surrounding vegetation. Large macaw aggregations did not form on the lower portion of the lick. The parakeet aggregation used the far left edge of the lick almost exclusively. This section had exposed clay 8.6 to 16 m high and trees immediately adjacent to it.

Lick Use by Other Psittacines.—The White-bellied Parrot was uncommon on the lick (Table 1). It was difficult to detect when arriving, but apparently arrived in groups of up to 10 (Gilardi and Munn 1998; DJB, pers. obs.). This species did not depend on joining with other birds to use the lick. Small groups perched in the trees on the left edge of the lick and remained vigilant while a few individuals at a time descended to the lick (2.8 ± 2.0 individuals, n = 23). This species usually used the lick in monospecific groups (47%) or with the parakeet aggregation (36%, Table 1). This species also use the lick until ~1,000 hrs, well after termination of the early morning activity (Brightsmith 2004).

DISCUSSION

Aggregation Membership.—Clay lick use was dominated by large mixed species aggregations.
and all 13 psittacine species regularly joined at least one of the three types of mixed species aggregations. These aggregations were not observed away from clay licks except for casual associations of large macaws at fruiting trees (Gilardi and Munn 1998; A. T. K. Lee, pers. comm.). Group sizes at clay licks were much greater than those of birds away from clay licks (Gilardi and Munn 1998) and <1% of lick use was by lone individuals. These data suggest that birds adopt novel behavioral strategies when using clay licks.

Stratification by size was clear among the mixed species aggregations: (1) large macaws, (2) large parrots and small macaws, and (3) parakeets and small parrots (Table 1). Species may segregate by size as heavier species take flight slower, accelerate slower, and have wider turning radii making them stragglers when mixed species groups flee from aerial predators. Direct competition should also favor size stratification as aggressive interactions are common on clay licks: smaller species are usually displaced by larger species but numerically dominant smaller species can exclude larger species if the size difference is not too great (Burger and Gochfeld 2003). Thus, predation may select against larger species joining smaller ones while competition may select against smaller species joining larger ones. This may explain the relative uniformity of body size among aggregation members.

The cost of ‘false alarms’ may also be important in shaping foraging behavior and aggregation composition, as disturbances reduce foraging efficiency (Sirot 2006, Beauchamp and Ruxton 2007). Over 90% of the flights from the lick in our study had no apparent cause suggesting a high rate of false alarms. Smaller species have a higher risk of predation and expend less energy each time they fly from the lick, and should have a lower alarm threshold, give more unnecessary alarm calls, and have correspondingly higher rate of departures from the lick. Members of an aggregation often respond to alarms as a group and larger species may have greater energy expenditure when using the lick alongside more ‘flighty’ smaller species. This also favors formation of aggregations of similar sized individuals.

The coloration of the species in each aggregation was similar; the three large macaw species in flight were a mix of red, blue, green, and yellow while the large parrot and parakeet aggregations were composed predominantly of green birds with dark green, blue or black heads and primaries. The formation of homogeneous groups (in size and color) is predicted where predators attacking groups focus on visually aberrant individuals (Landeau and Terborgh 1986, Theodorakis 1989, McRobert and Bradner 1998, Hoare et al. 2000).

The large macaws that occasionally join the large parrot aggregation are a notable exception to the tendency for visually similar individuals to join together on clay licks (see also Mee et al. 2005). However, when large macaws join the large parrots they usually do not integrate into the center of the group. Instead, they use the highest parts of the lick, ~ 3 m above the center of the aggregation, where the soil quality is inferior (i.e., 50 to 75% less sodium), but where they have the best chances for rapid escape (Brightsmith et al. 2008; DJB, unpulh. data). The large macaws at Tambopata Research Center spent <10% of their total lick use in the presence of the large parrot aggregation. In addition, large macaws rarely join parrot aggregations at other clay licks and instead usually use licks during the late mornings and afternoons (Burger and Gochfeld 2003; DJB, unpulh. data). Why large macaws join parrot groups is unclear, but it may be because their large size makes them vulnerable to a smaller number of raptor species, and because early morning is the only time when lick use is temporally predictable. Large macaws during the rest of the day may wait near the lick for up to 3 hrs before a group successfully initiates lick use.

White-bellied Parrots were least likely to join mixed species groups and were the most visually distinct small parrot at the site. They are green with a bright yellow head when seen in flight from above and behind while all other local species are green and have green, dark blue or black heads. However, both the large macaws and White-bellied Parrots are likely using the best of the available options for lick use and probably benefit from joining mixed species groups as even ‘oddballs’ receive protection from predators when group sizes are sufficiently large (Landeau and Terborgh 1986).

Lick use aggregations similar in structure to those at Tambopata have been documented by Burger and Gochfeld (2003) at a lick 250 km to the west and by DJB at numerous other licks throughout southeastern Peru. The similarities in behavior observed across these localities suggest that generalizations discussed here may apply to avian aggregations at many geophagy sites.
However, there is evidence that group composition, relative abundance, and timing of lick use vary among sites (Mee et al. 2005) suggesting birds may be responding to a variety of undocumented site-specific circumstances. Comparative studies would be highly informative.

Only three of 13 parrot species used the clay lick in cohesive monospecific groups: White-eyed Parakeet, Dusky-headed Parakeet, and White-bellied Parrot. These species, when not using the clay lick, normally occur in the largest monospecific groups of the 13 species (Gilardi and Munn 1998, Table 3). Other psittacines in the region, Cobalt-winged Parakeets (Brotogeris cyanoptera), Rose-fronted Parakeets (Pyrrhura roseifrons), Black-capped Parakeets (P. rupicola), and Dusky-billed Parrots (F. modestus) also occur in large groups away from clay licks and initiate lick use in monospecific groups (Gilardi and Munn 1998; DJB, unpubl. data). These findings suggest there is a causal link between species’ intraspecific sociality and monospecific lick use.

Arrival and Descent to the Lick.—Animals approaching geophagy sites are normally wary (Izawa 1993). The two approach behaviors we documented, slow circular flights and moving deliberately through adjacent trees likely serve to (1) check the lick area for predators, (2) watch for landslides, and (3) recruit individuals to the lead group. Birds would break off their approach or shift to alternative areas of the lick when predators or landslides were detected. Parrots would also break off their approach if the first group was not joined by others.

Spatial Distribution.—Bird use was confined to four small areas of the cliff even though the soil was usable across the majority of the lick (DJB, unpubl. data). This suggests the pressure to congregate (as protection from predators) is stronger than the pressure to disperse across the lick (likely due to competition). The large macaws used the highest and most open areas of the clay lick most frequently while the smallest species used the areas closest to cover. This is similar to findings from previous studies (Burger and Gochfeld 2003, Mee et al. 2005). Why lick site selection varies with body size is unknown, but likely relates to methods of approaching the lick and avoiding predators displayed by the different species.

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LITERATURE CITED


Vocal Repertoire of the Yellow-Faced Parrot (*Alipiopsitta xanthops*)

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**ABSTRACT**—We describe the vocal repertoire of the Yellow-faced Parrot (*Alipiopsitta xanthops*) from recorded vocalizations and also flock sizes in Brasilia (Brazil) during 2006. Vocal communication signals are both long-range and short-range sounds. We describe seven call types: flight call (long-range), long-range alarm call, congregation call (long-range), two agonistic calls (long-range/short-range), sentinel call (short-range), and a short-range alarm call. The flight call is equivalent to the functional song and contains the species-specific recognition code. Flight calls may also be uttered when perched and, when in quick series, function as long-range alarm calls. Long-range alarm calls become a high intensity congregation signal when several individuals overlap and, despite degradation and attenuation, may contain the species-specific code over distances of 800 m. The average (±SD) feeding flock size was 7.7 ± 8.2 individuals (n = 116) while the roosting flock size was 79.1 ± 10.5 individuals (n = 7). Short-range calls maintain communication while minimizing detection. High intensity vocalizations allow long-range communication, improving feeding efficiency through use of large areas and stimulating late afternoon roost congregations. Low intensity vocalizations maintain communications without providing the position of the parrot. Received 22 June 2010. Accepted 9 February 2011.

Communication, as defined by Weaver (1949), is the procedure in which one mind may affect another. This broad definition is useful for communication studies, as it presumes a response by the message recipient, which may at times be observed and confirmed. Thus, it is possible to describe the meaning of a message by observing the behavioral responses to specific calls and, by recording these calls, the acoustical code.

Psittacids may use acoustical communication to signal danger, resource availability, flight cohesion, social status, congregation, and individual signature (Fernandez-Juricic et al. 1998a, b; Fernandez-Juricic and Martella 2000; Wanker and Fischer 2001; Marler 2004; Moura 2007). Vocal repertoire descriptions of Blue-crowned Parakeet (*Aratinga acuticaudata*) and Turquoise-fronted Amazon (*Amazona aestiva*) in Argentina (Fernandez-Juricic et al. 1998a, b; Fernandez-Juricic and Martella 2000) reveal a communication system in which each vocalization has a specific function such as alarm, contact, agonistic interactions, and flying. The Orange-winged Amazon (*A. amazonica*) has similar vocal repertoire components (Moura 2007). For instance, there are three kinds of alarm calls with specific contexts: indication of predator location, indication to a nesting partner that it should not leave the nest due to a threat, or a simple fly-away message.

Psittacids present great flock size variation throughout the year. Nesting pairs are usually isolated until gathering after reproduction (Seixas 2009, Moura et al. 2010). Flock size variation may even occur during the day to improve feeding efficiency (Chapman et al. 1989; Paranhos et al. 2007, 2009; Seixas 2009; Tubelis 2009), as small flocks may be more efficient in resource-limited localities. However, these birds roost in great numbers at night (Carrara et al. 2007). This brings the necessity of an efficient way of flock congregation and several species use special calls to congregate at sheltered roosting places (Marler 2004).

The Yellow-faced Parrot (*Alipiopsitta xanthops*) is a Cerrado endemic with a wide distribution from the southern part of the State of Maranhão throughout central Brazil to north of the states of São Paulo and Mato Grosso do Sul, and Bolivia (Forshaw 1989). Vielliard (1994) analyzed the flight call of this species for phylogeny purposes, but a complete analysis of its repertoire has not been completed. Communication may have an important role on how parrots use habitats, and it is important to know the function of the vocal repertoire in the wild. Our objectives were to: (1) describe the vocal repertoire of the species, and
METHODS

Study Area.—The study was conducted between January 2006 and January 2007 at Brasília, DF (15° 47’ 07” S, 48° 02’ 02” W). We sampled during early morning (0600–1000 hrs) and in the late afternoon (1600–1830 hrs). The area consists of sensu strictu Cerrado, savanna-like vegetation common in central Brazil.

Flock Size.—We recorded flock sizes during the morning, when flocks were flying or feeding (feeding flocks), and also in the late afternoon, during roosting preparation (roosting flocks). We also recorded flock size during feeding (feeding flocks) at four different plants: Eriotheca pubescens (Bombacaceae), Qualea parviflora (Vochysiaceae), Caryocar brasiliense (Caryocaceae), and Mimosa claussenii (Mimosaceae). Mimosa claussenii, the smallest, has a maximum trunk diameter of 11 cm (Silva-Junior 2005) and maximum height of ~3 m (CBdeA, pers. obs.) The other three plants had larger sizes, reaching ~8 m. Eriotheca pubescens has a trunk diameter up to 85 cm, Qualea parviflora = 65 cm, and Caryocar brasiliense = 68 cm (Silva-Junior 2005). We compared flock size of parrots using M. claussenii with flock sizes of parrots using the larger trees with a unilateral U-test (Biostat 5.0) (Ayres et al. 2007), assuming that large flocks are unsuitable in small trees and, therefore, flocks feeding on M. claussenii should be smaller.

Acoustical Communication.—We recorded vocalizations using a parabola, a Shure Beta-58 cardioid microphone, and a Nagra-E analog recorder. Recordings were made on magnetic tape with a speed of 19 cm/sec, and digitized with a 24-bit and 44.1 kHz resolution. We used Cool Edit Pro 2000 for the analysis (FFT sample size of 512).

We were able to relate the physical characteristics of the calls with the message meaning through sonograms and response observations, based on Weaver’s (1949) broad definition of communication. We measured: call duration, minimum and maximum fundamental frequencies, and fundamental frequency bandwidth used to physically describe each call. Some calls presented pseudo pulses (very short sound with a low frequency resolution), in which case we also measured the number of pseudo pulses and pseudo-pulse rates. Pulse rates were measured in pulses per second (Hz). The recordings are deposited at the Neotropical Sound Archive (ASN) at the University of Campinas (Unicamp).

We observed large variations in sound intensity during the analysis. The relative intensities were measured whenever the same individual emitted two different vocalizations. We only used recordings of a single calling individual to assure that we were using the same individual for this analysis. We used a single individual at first for measurements of congregation calls for comparison with the group congregation call. We amplified the track until its peak reached 0 dB, and then measured the intensities of each call type. Data are presented as means ± SD.

RESULTS

Flock Size.—Flocks of Yellow-faced Parrots arrived at the study site from Brasilia National Park (4 km distant) during early morning. Feeding flocks had 7.7 ± 8.2 individuals (n = 116 flocks). Flocks flew southeast of the area and we lost track of them at about 1000 hrs. Feeding flocks returned to the area and gathered during late afternoon. A single large roosting flock departed for Brasilia National Park just before nightfall. Roosting flocks could be as large as 90 individuals, and had 79 ± 10.5 individuals on average (n = 7 flocks). Feeding flocks varied from a single individual to 40 individuals feeding in the same tree (8.9 ± 8.8, n = 89 flocks). Feeding flocks were not as large as roosting flocks.

Feeding flock size varied according to plant species. Flocks were larger during use of larger trees (Qualea parviflora, Eriotheca pubescens, Caryocar brasiliense) when compared to Mimosa claussenii, (unilateral U-test P < 0.05 for all comparisons).

Acoustical Communication.—We analyzed 160 min of recordings which were visually selected based on degradation and signal to noise ratio. We ignored noisy and low-level recordings. Several repertoire components were found for the species. Communication was divided between long-range and short-range signals, based on high and low amplitude sounds, respectively.

Flight Call.—This vocalization was common during observations (Fig. 1A). Individuals were often heard vocalizing during flight but also when perched. The call is equivalent to the functional song, which carries the species-specific recognition code. The call has a fundamental frequency between 0.5 and 1.5 kHz, and duration of 240 ms.
FIG. 1. Yellow-faced Parrot repertoire in Brasilia: (A) flight call; (B) long-range alarm; (C) agonistic vocalization I; (D) agonistic vocalization II; (E) sentinel call; (F) the two notes of short-range alarm call.

It may help maintain flight cohesion, indicating individual positions during flight. We also heard solitary individuals uttering this vocalization, possibly seeking other individuals in the area, indicating a contact message. The emission rate of the call was 0.69 ± 0.32 Hz ($n = 34$ calls from 8 individuals). This call also caused interspecific responses, as we observed individuals of the Turquoise-fronted Amazon responding to the call, leading to a mixed-flock formation.

**Long-range Alarm Call.**—This type of vocalization was common throughout the year (Fig. 1B). It was heard during flight or while perched, as a response to the approach of predators such as Southern Crested Caracara (*Caracara plancus*), or even during the approach of the observer. It consists of a quick series of flight calls. The emission rate of this call is 2.61 ± 0.61 Hz (30 calls from 7 individuals), over three times higher than the flight call ($U$-test $P < 0.0001$).

**Congregation Call.**—The call is composed of the long-range alarm call uttered by several individuals with substantial overlap. This creates a noisy sound of great intensity, but with species recognition quality. Distant flocks were observed responding with the same vocalization. It was common to observe flocks congregating on a tree after a few repetitions, or even clustering during flight. This response indicates a flock cohesion function by giving flock location at great distances. We were able to visually locate feeding flocks on a map using visual clues as trees, fences, and crops. The maximum communication range was 800 m. However, distances were only registered when both flocks were heard and seen at ground level by the observer, and with medium size flocks. Thus, the communication range might be greater.

**Agonistic Vocalization I.**—This vocalization was observed during feeding, when individuals perched close to each other (Fig. 1C). When a flying parrot perched too close to an already perched parrot, the perched parrot would open its wings and emit this highly modulated and harmonically rich call. The fundamental frequency decreases from 4 to 1 kHz, and the call has a duration of 171 ms (Table 1). The response to this call was to fly, usually together with agonistic vocalization II. The events could happen in inverse order, and agonistic vocalization I could be uttered only after agonistic vocalization II. We considered this call to be part of the long-range repertoire due to the high sound intensity, although the message recipient was at close range.

**Agonistic Vocalization II.**—This call is closely associated with agonistic vocalization I, but its intensity is ~11 dB lower (Fig. 1D). It seems to calm the parrot that uttered agonistic vocalization I. It consists of a six pseudo-pulse trill with fundamental frequency of 1 kHz and duration of ~100 ms (Table 1). We also observed this vocalization being uttered before agonistic vocalization I. The perching individual possibly sought to avoid any discomfort caused by its proximity to the already perched parrot.
Sentinel Call.—This vocalization was heard only during feeding (Fig. 1E). It was common to observe one or two individual sentinels, perched on top branches, emitting these sounds while observing the surroundings. The rate of emission was quite variable. Calling rates reached two calls/min using a 5-min recording. It has fundamental frequencies between 0.7 and 1.2 kHz and duration of 120 ms (Table 1). This vocalization appears to inform the presence of a sentinel to other flock members, as visual contact may not be possible in dense trees. Other calls were also heard during feeding, but it was not possible to describe the response, as there were too many, and we had great difficulties recording them within the feeding context.

Short-range Alarm Call.—This vocalization was rarely heard, and is quite different from the long-range alarm call (Fig. 1F). However, the response to this message was clear. As a response to this call, signaled by a flying individual, a perched parrot would fly silently, due to a danger situation. It has short range and does not give away the parrot's position, allowing furtive flight. Trees rapidly block the view of flying parrots and make it difficult to locate them. The fundamental frequency is between 0.8 and 1.5 kHz and duration ~180 ms (Table 1). At times, it was uttered with a preliminary note. However, the low quantity and quality of the recordings did not allow us to fully understand the preliminary note function, nor if it could alter the response of the recipient parrot. We recorded it on five occasions, usually with low quality. However, we made other observations of the same reaction following this call.

Amplitude Comparisons.—Call intensity comparisons revealed a great amount of variation between calls. Long-range alarm calls were 14.7 dB louder than sentinel calls ($U$-test $P < 0.001$). Agonistic vocalization I was 11 dB louder than agonistic vocalization II ($U$-test $P < 0.001$). Congregation long-range calls can be 10 dB louder than long-range alarm calls; however, as relative intensity estimates of long-range alarm calls were made using medium size feeding flocks, differences of intensity could be greater for roosting flocks.

DISCUSSION

The Yellow-faced Parrot repertoire has a clear division between short- and long-range calls. Fernandez-Juricic (1998a) used the term 'guttural vocalizations' for short-range vocalizations in the Turquoise-fronted Amazon. We prefer to use long-range or short-range vocalizations, as guttural refers to the timbre and not range, and range has a major role in parrot communication. We also observed other species with long-range/short-range communication, including Red-shouldered Macaw (Diopsittaca nobilis), Peach-fronted Parakeet (Aratinga aurea), Yellow-chevroned Parakeet (Brotogeris chiriri), Blue-and-Yellow Macaw (Ara ararauna), and Turquoise-fronted Amazon. Proper repertoire descriptions are necessary to fully identify the scope of long-range communication in Psittacidae. These studies should include sound intensity and decay measures, so we could fully comprehend the mechanism used to attain higher ranges, and its peculiarities among different species.

Flocks were constantly dividing and regrouping during feeding (feeding flocks). At night, a large flock was formed to roost (roosting flocks). Our data are consistent with those of Carrara et al. (2007) for the Yellow-faced Parrot, where maximum flock sizes were only achieved during preparation for roosting. Parrots were observed foraging in flocks rarely larger than 20 individuals, while flocks of up to 160 individuals were observed during roosting congregation. Our data suggests feeding may have a central role in this pattern, as it indicates a direct relation between flock size and tree size. Other studies of different
Communication, as it is the mechanism that allows these programs should also consider acoustical areas used by parrots, as parrots could guarantee congregation calls. Flock cohesion is long-range acoustic communication, through use of flight or higher range traffic near conservation areas. The congregation system used by Yellow-fac ed Parrots is long-range acoustic communication, and feeding efficiency of Yellow-fac ed Parrots. Noisy environments may not be suitable for species conservation, and care should be taken to avoid building roads for heavy traffic near conservation areas.

Short-range calls allow information exchange at close range as their low intensity reduces detection. This feature seems to be advantageous, as Yellow-faced Parrots usually remain hidden while perched (Sick 2001). The presence of a large short-range repertoire (CBdeA, pers. obs.) indicates substantial information exchange during feeding. Unlike White-vented Violet-ear (Colibri serrirostris), where the song complexity could be responsible for male selection by females (Silva and Vielliard 2006), each note of Yellow-faced Parrots seems to have a precise meaning, and a precise behavioral response. Thus, the interpretation of repertoire size should be different for parrots. However, we were not able to describe its full short communication repertoire, as we depended on behavioral responses that are not always observed.

Foraging flocks split and congregated constantly. Long-range communication is essential to flocks congregation and flight coordination. The intensity of the call also has a major role, as it correlates to the range at which it is heard. There is a great amount of intensity variation involved in the repertoire of the Yellow-faced Parrot. The long-range alarm call is 14 dB louder than sentinel calls. Flock cohesion is attained through long-range alarm call overlap, and may be 10 dB louder. As a consequence, the flock cohesion call can be 24 dB louder than sentinel calls, corresponding to a range ~16 times greater (Backus 1977), and a detectable area 256 times larger. Flock cohesion high intensity calls are achieved through individual long-range alarm call overlap and, the louder the congregation call, the larger the flock size. Parrots, when in small flocks, use low intensity sounds, maintaining communication while reducing detection.

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LITERATURE CITED


ABSTRACT.—We studied seasonal profiles of circulating testosterone concentrations among male and female adult Tree Swallows (Tachycineta bicolor) breeding in nest-box colonies near Ames, Iowa, USA. Mean plasma testosterone in males was elevated during nest establishment (0.63 ± 0.86 ng/ml) and incubation stages (0.28 ± 0.26 ng/ml), and was significantly lower after hatching (0.03 ± 0.05 ng/ml) when males began provisioning nestlings. Male swallows do not incubate and high testosterone during the incubation stage may facilitate pursuit of extra-pair matings. Female testosterone concentrations were an order of magnitude lower than those of males (nest establishment, mean = 0.06 ± 0.09 ng/ml) and did not change significantly over the breeding season. These testosterone profiles support the hypothesis that elevated testosterone in males is associated with defense behaviors and obtaining additional mating opportunities during the first part of the breeding season, but is incompatible with parental care once the eggs have hatched. Received 8 September 2010. Accepted 19 March 2011.

Androgens such as testosterone promote secondary sex characteristics, sperm production, and aggressive behavior in male birds. Elevated circulating testosterone increases song production, mate guarding, and pursuit of extra-pair mating opportunities by males while also decreasing parental behavior (reviewed in Lynn 2008). Testosterone concentrations in temperate zone-breeding passerines generally are highest at the start of the breeding season when males compete for territories and mates, but this pattern varies with mating system and whether or not the male participates in parental care (Wingfield et al 1990). For example, hormonal correlates of parental and sexual behavior have been studied in two closely related species: Blue-headed Vireo
Both Blue-headed Vireos participate in nest construction, incubation, and provisioning young and do not have a pre-nesting peak in testosterone. Male Red-eyed Vireos, however, exhibit parental care only after nestlings are present, and circulating testosterone is elevated early in the nesting season, but declines by the nesting stage (Van Roo et al. 2003).

We examined temporal profiles of plasma testosterone in male and female Tree Swallows (Tachycineta bicolor) during the breeding season. Tree Swallows are socially monogamous and secondary cavity nesters. There is competition for typically scarce natural nesting sites, which are defended by both males and females (Holroyd 1975, Winkler 1992). Males contribute to nest building, do not incubate, but contribute about equally to provisioning nestlings (Quinney 1986). If either the male or female parent is lost, the remaining parent will increase their nestling food provisioning rate. This increase neither fully compensates for loss of the other parent nor can it be sustained for an extended period of time, resulting in reduced reproductive success (Leffelaar and Robertson 1986). Males and females also have unusually high rates of extra-pair fertilizations for a socially monogamous species. Whereas extra-pair paternity rates in socially monogamous species in general average 18.7% of broods and 11.1% of offspring (reviewed in Griffith et al. 2002); 50-87% of broods in nest box populations of Tree Swallows contain extra-pair young and extra-pair males father 38-53% of the offspring in those broods (Barber et al. 1996). Testosterone is thought to influence the tradeoff between behaviors that facilitate obtaining additional mating opportunities versus investing in offspring care (Raouf et al. 1997). We predicted testosterone concentrations would be highest in males during nest establishment and would remain elevated during incubation when males can obtain extra-pair matings. Their testosterone concentrations should decrease when eggs hatch and males begin provisioning nestlings.

Both male and female Tree Swallows defend the nest, although males have a greater maximal alarm call-rate and longer call duration compared to females. Several other defense measures including number of dives towards predators and time defending the nest do not differ between males and females (Winkler 1992). Elevated female aggression has been associated with peaks in female testosterone concentrations in other species (Cristol and Johnsen 1994, Woodley and Moore 1999). However, females displaying aggressive behavior do not always have a corresponding increase in testosterone (Elekonich and Wingfield 2000, Jawor et al. 2006). We predicted testosterone concentrations in female Tree Swallows would be lower than those of males, but would be elevated during the territory and nest establishment phase and decline once incubation began.

METHODS

Field and Laboratory Procedures.---We collected blood samples to assay testosterone concentrations from Tree Swallows using nest boxes near Ames, Iowa, USA, (42° 01' N, 93° 37' W) in May-June 2009. Boxes were spaced ~20 m apart, and there was considerable interaction (nest box and mate guarding) among breeding birds. We captured 25 male and 30 female adult Tree Swallows during three time periods: pair bond and nest-box establishment (hereafter nest establishment), incubation, and the nestling stage. We caught individuals during nest establishment either with mist nets or upon entrance into a nest box during nest building. Not all females had brood patches at this stage, and we classified individuals based on the presence of a cloacal protuberance in males or the brown plumage of second-year females. We confirmed our classification for seven of 10 females and three of seven males through later recapture at a nest, data from previous years, or wing length in the predominantly female (<113 mm) or male (>122 mm) ranges (Stutchbury and Robinson 1987). We caught all birds during the incubation and nestling stages using nest-box traps. Males and females were easily distinguished during these two stages based on presence of a brood patch in females. Each bird was sampled only once.

We took a blood sample of ~100 µl within 5 min of capture from a wing vein, collecting blood into heparinized capillary tubes that were immediately cooled on ice. We separated plasma from cells by centrifugation within 4 hrs and stored the plasma at ~80 °C. We measured plasma testosterone in duplicate using a radioimmunoassay kit (DSL-4100) from Diagnostics Systems Laboratories (Brea, CA, USA) in September 2009. This RIA kit measures testosterone...
concentration in plasma directly using \( I^{125} \) labeled testosterone. The kit was modified by running all volumes at 25% of the suggested kit volume. Samples were run in two separate assays. The intra-assay and inter-assay coefficients of variation were 0.11 and 0.07, respectively.

We calculated the time in days relative to the initiation of laying in that bird’s nest for each sample. We assumed egg-laying began on the mean date of initiation of laying for the colony (18 May) for individuals sampled prior to egg-laying that did not remain to nest in our colony (n = 11). Varying this estimated egg lay date by ±7 days did not affect our results significantly. Incubation in Tree Swallows typically begins with the penultimate egg (~4–5 days after laying initiation) and hatching occurs ~14–15 days after the onset of incubation (Zach 1982).

### Statistical Analyses

Plasma testosterone concentrations were not normally distributed and we log-transformed testosterone concentrations for all statistical analyses. We performed an analysis of variance with plasma testosterone as the dependent variable using a model that incorporated time in days relative to the first egg, males or females, and the interaction between the two variables. There was a significant interaction between males or females and time relative to egg lay; thus, we used separate Tukey-Kramer honestly significant difference (HSD) tests to compare mean testosterone concentrations among the different breeding stages for males and females. We used JMP statistical software for all statistical analyses (SAS Institute Inc. 2009).

### RESULTS

Circulating testosterone concentrations in Tree Swallows ranged from 0.01 to 2.4 ng/ml in males and 0.01 to 0.23 ng/ml in females during the breeding season (Fig. 1). Gender \((F_{1,53} = 12.7, P = 0.0008)\), days relative to the first egg \((F_{1,53} = 5.7, P = 0.006)\), and the interaction between the two variables \((F_{1,53} = 4.9, P = 0.01)\) significantly affected testosterone concentration. Testosterone concentrations over the breeding season were about an order of magnitude higher in males than in females (male mean = 0.27 ng/ml; female mean = 0.03 ng/ml).

Circulating testosterone concentrations of males during the nest establishment stage did not differ from those during the incubation stage, but male testosterone concentration decreased significantly (Tukey-Kramer HSD, \( q = 2.5, p < 0.05 \)) during the nestling stage (Table 1). Mean testosterone concentrations of females did not differ significantly among different breeding stages.

### Table 1. Mean testosterone (T) concentrations in adult male and female Tree Swallows during three stages of the breeding season in nesting colonies near Ames, Iowa, USA.

<table>
<thead>
<tr>
<th>Breeding stage</th>
<th>Mean ± SD T (ng/ml)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest establishment</td>
<td>0.63 ± 0.86*</td>
<td>7</td>
</tr>
<tr>
<td>Incubation</td>
<td>0.28 ± 0.26*</td>
<td>7</td>
</tr>
<tr>
<td>Nestling care</td>
<td>0.03 ± 0.06*</td>
<td>11</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest establishment</td>
<td>0.06 ± 0.09*</td>
<td>10</td>
</tr>
<tr>
<td>Incubation</td>
<td>0.01 ± 0.01*</td>
<td>11</td>
</tr>
<tr>
<td>Nestling care</td>
<td>0.02 ± 0.02*</td>
<td>9</td>
</tr>
</tbody>
</table>

*Breeding stages with different superscripts have significantly different mean testosterone (T) concentrations in Tree Swallows (Tukey-Kramer HSD, \( q < 0.05 \)).
not differ significantly among breeding stages ($P > 0.05$).

**DISCUSSION**

Concentrations of circulating testosterone of male Tree Swallows were much higher than those of females, as expected, and particularly during the nest establishment and incubation stages. Testosterone did not decrease significantly in males until they began provisioning nestlings, when it was similar to that of females. Contrary to our predictions, we did not find evidence that females have elevated testosterone during nest establishment despite their active participation in nest defense (Winkler 1992). Rather, testosterone concentrations in females were generally low throughout the breeding season.

Bishop et al. (1998) measured testosterone in Tree Swallows in Ontario, Canada, during incubation (females only) or chick rearing (males only). They used a different assay and reported average values that were significantly higher than ours (~2.5 ng/ml in males and 0.9 ng/ml in females). Whether these differences are due to methodology (Bishop et al. 1998 measured testosterone after ether extraction whereas we measured it directly in plasma) or whether population differences exist is not known. Differences in seasonal testosterone patterns have been reported between populations of other species. Male Orange-crowned Warblers (*Oreothlypis celata*) in Alaska have a pre-incubation peak in testosterone and subsequent decline during incubation and nestling stages. In contrast, males on Catalina Island, California have elevated testosterone throughout the breeding season (Horton et al. 2010). Variation in testosterone profiles also occurs among Cliff Swallow (*Petrochelidon pyrrhonota*) populations, depending on breeding density (Smith et al. 2005).

We found testosterone was always low in female Tree Swallows. Elevated testosterone during nest stages that require parental behavior is frequently associated with negative consequences for reproductive success or other costs. For example, artificially elevating testosterone in female Dark-eyed Juncos (*Junco hyemalis*) resulted in delayed onset of egg laying after nest completion as well as lower body mass and delayed molt (Clotfelter et al. 2004, Zysling et al. 2006). Additionally, Zysling et al. (2006) found a negative correlation between cell-mediated immune function and total testosterone in female Dark-eyed Juncos. Veiga and Polo (2008) reported similar results in female Spotless Starlings (*Sturnus unicolor*), in which testosterone-treated females delayed egg laying, laid fewer eggs, and provisioned nestlings at a reduced rate in comparison to controls. Similarly, testosterone supplementation in males is known to disrupt or decrease parental behavior in many species (reviewed in Vleck and Vleck 2010). For example, male House Sparrows (*Passer domesticus*) supplemented with testosterone during chick rearing have reduced feeding rates and lower breeding success (Hegner and Wingfield 1987).

The low circulating testosterone concentrations we measured in both male and female Tree Swallows during the nestling stage likely reflects the importance of parental care by both members of the pair for optimizing reproductive success (Leffelaar and Robertson 1986). However, low testosterone is not an absolute requirement for the exhibition of parental care in some species, indicating some behavioral insensitivity to testosterone is possible (Van Duyse et al. 2000, Lynn et al. 2002). Hau (2007) suggested the negative effects often seen with elevated testosterone may be avoided if selection acts on the responsiveness of target tissues to testosterone. Additionally, McGlothlin et al. (2007) suggested the ability to produce short-term increases in testosterone may allow for temporary shifts in territorial and sexual behaviors without compromising overall parental care.

Decline in testosterone concentrations after egg laying may not be as critical for male Tree Swallows, which guard the nest but do not incubate, as for species in which the male incubates. There is a negative correlation between incubation behavior and testosterone concentrations in male European Starlings (*Sturnus vulgaris*) (Pinxten et al. 2007). Elevated circulating testosterone during the incubation stage may be beneficial to male Tree Swallows to facilitate extra-pair copulations (Raout et al. 1997). The date of egg laying can vary by as much as 7 weeks in our colonies because females that have lost their nest often lay a second clutch. Consequently other receptive females may be present after a male’s mate has begun incubation and may influence his testosterone level. A positive correlation between circulating testosterone in males and the presence of receptive females has been documented in other passerines such as European Starlings (Pinxten et al. 2003). Male
White-crowned Sparrows (Zonotrichia leucophrys) placed with sexually receptive females had higher plasma testosterone and exhibited greater copulatory behavior than those paired with non-receptive females (Moore 1983). The wide range of testosterone concentrations we found in male Tree Swallows (Fig. 1) may reflect variation in access to receptive females.

Our breeding season testosterone profile for male Tree Swallows supports the role of testosterone in behaviors associated with nest and mate defense, and obtaining additional mating opportunities through extra-pair copulations. The decrease in testosterone in males after eggs hatch, along with the continuously low testosterone profile in females, lends support to the predicted costs associated with possessing elevated testosterone, particularly those associated with simultaneously displaying parental behavior.

ACKNOWLEDGMENTS

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LITERATURE CITED


Bittner for invaluable help in the field.


ABSTRACT.—Nesting activity of the White-collared Swift (*Streptoprocne zonaris*) was monitored from October 2001 to March 2002 to describe the breeding chronology of this species. Data were obtained from the colony ‘La Cueva de los Pajaritos’, near Mallín, Córdoba, Argentina. These are the first descriptions of the nesting chronology of this species in Argentina. The breeding season lasted 81 days from egg laying in early November to fledging in middle to late January. Clutch size ranged from one to two eggs which were incubated for an average of 22 days. Nestlings remained in nests for an average of 44 days and fledglings remained at the nest for ~5 additional days. These observations provide new information on nesting sites used by *S. zonaris* in Argentina, and provide the first documentation of the length of the breeding phases for the species in South America. The ‘apparently shortened’ length of incubation and nestling periods may be a geographical effect, due to this being the most southeastern known breeding colony for *S. zonaris*. Received 6 July 2010. Accepted 7 February 2011.

Swifts (Apodidae) are difficult to observe and identify in the field. Access to nesting sites is usually complicated, and large gaps exist in our knowledge about the biology of many species (Whitacre 1989, Marín and Stiles 1992). The White-collared Swift (*Streptoprocne zonaris*) is in the subfamily Cypseloidinae that comprises 13 species of tropical swifts (Lack 1956, Sibley and Monroe 1990, Chantler and Driessens 1995, Chantler 1999, Mario 1999), Neotropical swifts breed early in the rainy season, coinciding with the peak of flying insects.

There is a lack of information about _S. zonaris_ particularly in Argentina. Most published records are distributional notes and nest descriptions (De la Peña 1982, De Lucca 1989, Biancucci 1995, Miattello et al. 1999). This species has been well documented in northern and western Argentina (Dabbene 1918, Olrog 1979, De Lucca 1989), and is known to occur in central and eastern Argentina (Narosky and Yzuríeta 1987). _S. zonaris_ is best documented in the Province of Córdoba (Pergolini 1944, De la Peña 1982, Narosky and Yzuríeta 1987, Yzuríeta 1995, Miattello et al. 1999) at the ‘La Cueva de los Pajaritos’ colony, where many swifts occur (Narosky and Yzuríeta 1987, Yzuríeta 1995). No current long-term study has been conducted on the reproduction of _S. zonaris_. The objectives of my study were to: (1) contribute to the general knowledge of the reproductive biology of swifts, and (2) delineate the breeding chronology of the White-collared Swift in Argentina.

**METHODS**

**Study Area.**—The Province of Córdoba occupies much of central Argentina at the confluence of many areas with different physiognomy and taxonomic lineages (Bucher and Abalos 1979). This region is in the Distrito Serrano Chaqueño (Chaco Province) with a semiarid climate influenced mainly by the Sierras Grandes (Cabrera 1976). These conditions relate to the rugged topography, insulation, and humidity, as well as the type of substrate and vegetation (Miattello et al. 1999). Low temperatures and northerly winds occur from June to late August, often associated with drought. Rain occurs mainly in summer ranging from 800 to 900 mm between October and April (Miattello et al. 1999). The study site is known as ‘La Cueva de los Pajaritos’ and is at 31°18' S, 64°34' W, 869 m asl.

**Field Work and Data Analysis.**—The study site was subdivided into four different areas along natural limits of the relief configurations: ‘Garajata del Diabla’, ‘Cabeza del Indio’, ‘Cueva de los Pajaritos’, and ‘Lluvia del Amor’. Field work was conducted for 6 consecutive months from October 2001 to March 2002, I made 18 visits, each 2 days in duration, three times each month. Field work was conducted for 6 consecutive months from October 2001 to March 2002, I made 18 visits, each 2 days in duration, three times each month at ~8-day intervals. Nest searching was conducted during each visit considering the variability of the encounter rate throughout the reproductive period (Ralph et al. 1996). Date, location, and place of settlement were recorded for each nest. Nests were recorded in the order in which they were found and were monitored at 0630–0930 and 1700–2000 hrs. The number of adults, eggs, and/or chicks present in or near the nest was recorded, and data on the physical appearance of nests were collected. I measured timing and duration of egg-laying, incubation, hatching, nestling, and fledging periods and, when necessary, these dates were calculated as averages between visits. The reproductive period of _S. zonaris_ was calculated from first egg-laying until last fledging, considering the activity of all nests (Marin 1999). Length of incubation and nestling stages was estimated following Foerster (1987).

**RESULTS**

**Nests.**—Six nests of _S. zonaris_ were found in three of the four subareas of the site, all in close proximity to water (Table 1). Nests were placed on horizontal or slightly inclined surfaces on the vertical walls of the cliffs. All sites were relatively inaccessible with three in small cracks of the walls and three on extended prominence platforms. Most nests had a well-defined shape, typically a ‘circular plate’ with a central depression. The exceptions were semicircular nest S5 and nest S6 that did not show evident material and which were too small to have a specific shape. Total or partial absence of nesting material was also recorded in nests (n = 2) inside ‘La Cueva de los Pajaritos’.

Nestling material was principally semi-wet mud mixed with varying amounts of living plants (mosses, pteridophytes), and roots of macrophytes. Nesting material was drier in nests (n = 3) in ‘Cabeza del Indio’ and ‘La Cueva de los

<table>
<thead>
<tr>
<th>Location</th>
<th># of nests</th>
<th>Nest code</th>
<th>Date found</th>
<th>Distance from water (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘Garganta del Diablo’</td>
<td></td>
<td>S1</td>
<td>30 Sep 2001</td>
<td>Waterfall 1, Creek 5</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>S2</td>
<td>30 Sep 2001</td>
<td>Waterfall 4, Creek</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S5</td>
<td>27 Dec 2001</td>
<td>Waterfall 10, Creek 4</td>
</tr>
<tr>
<td>‘Cabeza del Indio’</td>
<td>1</td>
<td>S6</td>
<td>06 Jan 2002</td>
<td>Waterfall 3, Creek 4</td>
</tr>
<tr>
<td>‘Cueva de los Pajaritos’</td>
<td>2</td>
<td>S3</td>
<td>30 Sep 2001</td>
<td>Waterfall 15, Creek 4, 5</td>
</tr>
<tr>
<td>‘Lluvia del Amor’</td>
<td></td>
<td>S4</td>
<td>13 Oct 2001</td>
<td>Waterfall 17, Creek 3</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pajaritos' where they also included some leaves of angiosperms.

**Breeding Chronology.**—The reproductive period of *S. zonaris* coincided with the rainy season. Egg-laying started with arrival of the first moderate rains (Oct and Nov). More intense rain occurred in January when fledglings were leaving nesting areas. Peak precipitation was recorded when the breeding season had ended in mid January.

Four active nests with 1–2 adults were found between late September and mid-October. Two other nests were found between December and January, each with two nestlings (Table 1). Nest S4 was not successful. The reproductive period of *S. zonaris* lasted 81 days from early November until mid to late January (Fig. 1).

**Egg Laying.**—The duration of this phase was estimated based on active nests (*n* = 5), although only two eggs were observed. These eggs were white in color and sub-elliptical in shape, and were deposited in the center of the nest. Egg laying occurred over 21 days from 1 to 21 November (Fig. 1); clutch size was one (*n* = 2) to two (*n* = 3) eggs.

**Incubation.**—Incubating adults were found during 41 days from early November to mid-December (Fig. 1). Eggs were incubated for an average of 22 days (range = 20–25 days) and were exposed on few occasions.

**Hatching.**—Hatching date was ascertained for nests S1 and S2, and estimated for nest S3. The remaining two nests were found in the nestling stage. Eggs in nest S1 hatched on the afternoon of

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**Fledging**

**Nestling**

**Hatching**

**Incubation**

**Egg Laying**

---

**Month**

TABLE 2. Breeding chronology and timing of reproductive stages of _Streptoprocne_ spp. swifts. I = early in month, M = middle of month, F = end of month, (−) = no available data, and (**) = calculated from data of hatch.

<table>
<thead>
<tr>
<th>Species</th>
<th>Latitude (Country)</th>
<th>Egg laying</th>
<th>Hatching</th>
<th>Fledging</th>
<th>Incubation</th>
<th>Age of nestlings at fledging</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. zonuris</em>*</td>
<td>10° N (Costa Rica)</td>
<td>F, Apr</td>
<td>F, May</td>
<td>M, Jul</td>
<td>30-35 days</td>
<td>45-55 days</td>
</tr>
<tr>
<td></td>
<td>16° N (Mexico)</td>
<td>F, Apr; I, May</td>
<td>F, Nov (Prob.)</td>
<td>I, Jan</td>
<td>23-25 days (prob.)</td>
<td>Approx.</td>
</tr>
<tr>
<td></td>
<td>31° S (Argentina)</td>
<td>F, Nov</td>
<td>F, Nov</td>
<td>I, Nov</td>
<td>20-25 days</td>
<td>40-48 days</td>
</tr>
<tr>
<td></td>
<td>31° S (Argentina)</td>
<td></td>
<td></td>
<td>F, May</td>
<td>24 days</td>
<td>40-48 days</td>
</tr>
<tr>
<td></td>
<td>25° S (Brazil)</td>
<td></td>
<td></td>
<td>I, Jun</td>
<td>24 days</td>
<td>24-42 days</td>
</tr>
<tr>
<td></td>
<td>18° N (Mexico)</td>
<td></td>
<td></td>
<td>M, Jul</td>
<td>26-24 days</td>
<td>37-43 days</td>
</tr>
<tr>
<td></td>
<td>10° N (Trinidad and Tobago)</td>
<td></td>
<td></td>
<td>M, Jun</td>
<td>22-23 days</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10° N (Mexico)</td>
<td></td>
<td></td>
<td>F, Aug</td>
<td>24 days</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I, Aug</td>
<td>26-24 days</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Approx</td>
<td>22-23 days</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Approx.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


24 November and in nest S3 on ~11 December, a period of 18 days (Fig. 1). At least one adult remained at nests S1 and S2 during hatching. Nestlings were naked with eyes closed and a pale pink body.

_Nestling._—Nests were occupied by nestlings during 58 days from late November to mid-January (Fig. 1). Nestlings remained in nests for an average of 44 days (range = 40-48 days). The shortest period was recorded for the single chick in nest S3, while the longest was for the two chicks in nest S1.

_Fledging._—Nestlings fledged in January over a time interval of 15 days (Fig. 1). First departure was at age 25-33 days. This was a temporary event and, after 2 hrs, fledglings reoccupied the nests. Fledglings were quiet and stayed close to the nests while they were outside. Adults were also observed inside or near the nests. Definitive departure occurred at age 35-43 days, although fledglings stayed near nests until leaving the breeding site at age 40-48 days. Contrary to first departure, fledglings were active outside the nests flapping their wings rhythmically and clinging to the wall without taking flight. Intense vocalizations were also recorded. No adults were observed inside or near the nests during these displays. Fledging asynchrony was recorded in nest S6 with a difference of 5 days between nestlings. Some adults and juveniles were observed at the study site during February and March. On these occasions, adults reoccupied nests, but juveniles did not.

DISCUSSION

The breeding chronology of the White-collared Swift was recorded in five nests, which is a considerable number, given the ecological complexity of swifts. Reproduction lasted ~2½ months, from egg laying in November to fledging in late January, and was similar to other _Streptoprocne_ swifts (Table 2).

Breeding occurred with seasonal rains as for other neotropical swifts (Snow 1962, Rowley and Orr 1965, Collins 1968, Ayarzagüena 1984, Marin and Stiles 1992). This could be interpreted as an adaptive behavior to take advantage of the maximum abundance of food (Marin and Stiles 1992). It has been suggested that reproduction by _Streptoprocne_ species with large body size would begin before the rainy season because, unlike other swifts, these species depend mainly on moisture to build and adhere their nests (Rowley and Orr 1965, Collins 1968, Foerster 1987, Marin and Stiles 1992, Pichorim 2002).

Eggs were similar to those reported in previous studies (Rowley and Orr 1965, Stockton de Dod 1979, De la Peña 1982, Marin and Stiles 1992,
The incubation period was 22 days for S. zonaris and apparently is the shortest within the genus (Table 2) and possibly for the Cypseloidinae. Hatching at the end of November coincides with that reported by De la Peña (1982) in Córdoba; this author found eggs in advanced state of incubation at the end of November. Development of nestlings was slow compared with other swifts, probably due to the wet and cold microclimates they select (Collins 1968, Marin and Siles 1992, Marin 1997b). The age of fledglings leaving the nest within Streptoprocne species is usually not less than 40 days (Table 2). All nestlings in my study fledged in early to mid-January displaying the same behavior as S. bicuculata (Pichorín 2002) and S. rutilla (Marín and Siles 1992). Departure may be based on acquisition of a given body mass and wing length (Marín and Siles 1992, Marín 1997b, Pichorín 2002).

This study provides new information about the breeding biology of S. zonaris in Argentina, and the first reports of the incubation and nesting periods for the species in South America.

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I thank Manuel Marín, Martín Irurondo, and Pablo Bolcato for their continued, critical, and affectionate way to teach. This work was supported by CONICET (Argentina) and benefitted greatly from comments by anonymous referees. I thank Lucas Plaides Ricci and family, and Nicolás Almirante for allowing me to conduct research on the study site. I thank the Butcher and Saravia families and all who provided information; Centro de Investigaciones de la Región Semiárida (CIRSA), Centro de Applied Zoology Córdoba, Ada Echevarría, Martín De la Peña, and Tito Naresky. I especially thank Federico Ríos, María Julia Cavallero, Alberto Didier, Carlos Passeggi, and Valeria Peña for helping me as field and logistic assistants.

LITERATURE CITED

Nesting of the Fulvous-breasted Flatbill (Rhynchocyclus fulvipectus) in Southeastern Peru

David Ocampo1,4 and Gustavo A. Londoño2,3

ABSTRACT.—The Fulvous-breasted Flatbill (Rhynchocyclus fulvipectus) has an Andean distribution from Colombia and Venezuela to northeastern Bolivia between 750 and 2,300 m elevation. We describe the nesting behavior, nest, eggs, and nestlings of this species in the buffer zone of Manu National Park at Cock of the Rock Field Station, Cusco, Peru, from August through December 2009. We monitored seven nests using data loggers to describe incubation patterns and conducted direct observations of provisioning behavior. The two-egg clutch size and pear-shaped nest structure were consistent with previous reports. Incubation lasted 24 days (n = 1) and nestlings were in the nest for at least 29 days. We only observed one parent incubating (presumably the female) with average nest attentiveness of 64%, which decreased as the incubation period progressed. The adult made 10 to 15 foraging trips per day (n = 21) during incubation, when it spent on average (±SD) 32.9 ± 2.8 min during incubation bouts and 23.1 ± 6.3 min during foraging bouts (n = 3 nests). Nestlings were able to regulate their body temperature after the feathers were fully developed; however, their body temperature (37°C) was lower compared to adults. We confirmed Rhynchocyclus nests exclusively along creeks or rivers and also revealed long incubation and nestling periods, which may be more common than expected in tropical mountain areas. There was a decrease in nest attentiveness through time, contradicting previous findings on neotropical passerine species. Received 27 September 2010. Accepted 27 February 2011.

The genus Rhynchocyclus encompasses four species distributed from southern Mexico to northeastern Bolivia, eastern Venezuela, and...
Brazil (Ridgely and Tudor 1994, Fitzpatrick et al. 2004). The genus *Rhynchocyclus* is in the Flatbill clade, which includes the genus *Tolmomyias* (Lanyon 1988, Tello and Bates 2007, Ohlson et al. 2008) as a sister taxon. The nests of both *Tolmomyias* and *Rhynchocyclus* have been described as pear-shaped structures with a tubular side entrance in the base made with sticks, fibers, and dry leaves (Parker and Parker 1982, Hilty and Brown 1986, Fitzpatrick et al. 2004, Greeney et al. 2004, Brumfield and Maillard 2007).

The Fulvous-breasted Flatbill (*Rhynchocyclus fulvipectus*) is commonly found close to rivers and small creeks in secondary montane forest and shubby edge vegetation between 750 and 2,300 m (Ridgely and Tudor 1994, Fitzpatrick et al. 2004, Schulenberg et al. 2007). It is known that clutch size varies from one to three eggs, which are white with reddish dots on the widest end (Sclater and Salvin 1879, Fitzpatrick et al. 2004, Greeney et al. 2004). The only information about the nestling period is from a nest found by Greeney et al. (2004) in Ecuador that had an incomplete incubation period of 18 days and a full length nestling period of 27 days. Despite the large distribution of this species in South America, it is uncommon throughout its range and its lethargic behavior may underlie the lack of nesting information for it (Hilty and Brown 1986).

Detailed studies about the nesting biology of any species of the genus *Rhynchocyclus* are lacking (Fitzpatrick et al. 2004); our study was designed to provide the first complete description of the nesting biology of the Fulvous-breasted Flatbill.

**METHODS**

**Study Area.**—This study was conducted in the Kusñipata Valley at Cock of the Rock Field Station in the buffer area of Manu National Park, Cusco, Peru (13° 0.39’ 19.40” S, 71° 3.29’ 48.50” W) from August through December 2009. The station is at 1,450 m in an Andean cloud forest with a canopy height of 25 m, average temperature of 18.3°C (min–max = 12.1 to 26.6°C), and average precipitation of 521 mm with a rainy season from November through April and a dry season from May through August.

**Nest, Eggs, and Nestling Measurements.**—We obtained measurements of the nests, eggs, and nestlings. We took internal and external measurements for five of seven nests, and described and weighed the different nest materials and layers. We measured the length, width, and mass of the eggs. We took daily morphological measurements of the nestlings that included wing and tarsus length, and body mass; we also made qualitative descriptions every other day. We measured nestling body temperature using a thermocouple (Onset Computer Corporation, Pocasset, MA, USA) that we inserted into the cloaca. Body temperatures were taken to estimate when nestlings were able to regulate their body temperatures (when they became endothermic). We measured body temperature as soon as we took each nestling from the nest after placing each nestling on a plastic lid for 3 min (to prevent variation in loss of body heat due to the ground being hot or cold). The thermocouple tip was cleaned with alcohol between measurements, and was coated with petroleum jelly to reduce stress created by insertion. We also conducted direct observations of provisioning for 1.5 hrs at one nest on 2 different days for a total of 3 hrs. All mass measurements had an accuracy of 0.05 g (FlipScale F2; My Weigh, Phoenix, AZ, USA) and measurements of length/width were taken with a caliper with an accuracy of 0.1 mm.

**Incubation Patterns.**—We monitored incubation behavior at three nests on different days for a total of 21 days using two thermal sensors. One of the sensors was placed under the eggs, providing incubation rhythm and nest microclimate information, and the second was attached to the external face of the nest wall, providing ambient temperature. Both sensors were connected to a U-12 HOBO data-logger (Onset Computer Corporation, Pocasset, MA, USA) programmed to record temperatures every minute.

**Incubation Rhythm Analysis.**—We quantified the length and number of temperature fluctuation events produced by foraging trips (cooling periods) and returning to the nest to incubate (warming periods), following Cooper and Miles (2005). This procedure allowed us to estimate nest temperature fluctuations, number and length of foraging and incubating trips, and percentage of time the adult was incubating the eggs (Londoño 2009).

**RESULTS**

We found seven nests of which six contained two eggs each and one had only one egg. Four nests were depredated and one nest was destroyed when the branch upon which it was built fell into the river. We found an empty nest on 20 October 2009 and 7 days later (27 Oct) the nest contained...
one egg; the second egg was laid the following day. The first egg hatched on 19 November and the second the following day, for an incubation period of 24 days. The nestlings died 15 days after hatch as a result of a landslide that knocked down the nesting tree. The other nest with eggs that was studied successfully hatched on 15 November, and the nestling was still in the nest on 13 December when we left the station; thus, the nestling period was at least 29 days.

Nest and Eggs.—All nests were hanging and attached to the end of tree branches above small creeks. The nest was a dome structure with a side entrance opening towards the ground. Nests had extra nesting material above the dome, changing the general shape of the nest to resemble the shape of a pear.

Nests were composed of two layers. The external layer, which included extra material attached mainly to the upper part of the nest, weighed (x ± SD) 100.1 ± 38.7 g (n = 3) and was composed mainly of long bamboo (Guadua spp.) fibers (60%) as well as mosses, fern leaves, and dry roots with pieces of bark (40%). The inner layer weighed 26.5 ± 16.3 g (n = 3) and was mainly composed of dry bamboo leaves (95%) and fine white roots (5%).

The average (± SD) height of the nest above water was 2.1 ± 0.4 m (n = 7). The external measurements of the nest were 147.5 ± 55.8 mm × 156.9 ± 43.0 mm × 179.6 ± 6.7 mm (length, width, and height, respectively; n = 5). The nest entrance was 44.4 ± 10.8 × 39.0 ± 10.5 mm (length and width, respectively; n = 5), average nest thickness was 23.6 ± 5.5 mm, and distance from the entrance of the vertical tunnel to the roof was 81.5 mm (n = 1). The length of the cup was 122.5 ± 19.3 mm (n = 5) and cup depth was 49.8 ± 8.2 mm. The extra nest material above the dome nest measured 206.6 ± 89.7 mm in length × 94.1 ± 20.1 mm in width.

Most eggs were white with small reddish dots at the larger end, but the eggs were entirely white in two clutches. The eggs measured 24.4 ± 0.6 × 16.8 ± 0.5 mm (n = 13) and fresh weight was 3.5 ± 0.3 g (n = 6).

Incubation Patterns.—The average nest temperature was 34.4 °C (22.1–41.7 °C) when the female was on the nest, and decreased to 29.8 °C (20.1–38.9 °C) during foraging bouts. We observed daily incubation patterns for 21 days at three nests. Generally, the incubating birds made their first daily foraging trip a few minutes after sunrise (between 0515 and 0639 hrs) and returned to the nest for continuous night incubation between 1609 and 1825 hrs.

We only observed one parent incubating the eggs (presumably the female, based on the low nest attentiveness, <85%; Deeming 2002); it made on average 12.6 trips/day (min-max = 10–15 trips/day, n = 21). Incubation bouts at one nest lasted on average 33.6 min (5–82 min, n = 265) and foraging bouts averaged 22.4 min (9–104 min). The number of trips increased at the first nest through time from 11 to 13 trips/day during the first 5 days to 12–15 trips/day during the last 10 days. The average duration of incubation bouts was similar during the 16 days the nest was monitored (34.2 ± 4.7 min) with a small decrease during the last 3 days (28.3 ± 3.2 min). The average duration of foraging trips varied little during the 16 days, but longer trips (up to 74 min) were recorded during the last few days, especially during the last 3 days (Fig. 1A–C).

The number of trips per day for the second nest during the last 3 days of the incubation period was 12, incubation bouts lasted on average 29.7 min (28–32 min), and foraging bouts lasted on average 29.9 min (11–104 min) (Fig. 1D). We observed 11.5 trips/day for the third nest with an average duration of incubation bouts of 34.7 (31–38 min) with foraging bouts lasting on average 17.6 min (10–30 min).

Average daily nest attentiveness was 64% and varied between 51 and 75% (n = 21). Nest attentiveness for the nest for which we had incubation data between days 7 and 22 of the incubation period was higher (66%; 65–68%) during the first 5 days and decreased during the last 10 days (63%; 57–67%). We documented low nest attentiveness for the second nest during the last 3 days of the incubation period; 55% (51–61%). The third nest had a nest attentiveness of 74–75% during 3 days before it was predated.

Nestlings.—The nestlings weighed 3.1 ± 0.4 g (n = 3) on day of hatch, the skin was pink-orange, the eyes were closed, and there was gray down on the back and wings. Pin feathers started to emerge from the skin 5 days after hatching and, 13 days after hatching, feathers started to emerge from the pins; feathers were yellow on the flanks and olive over the rest of the body. The feathers completely emerged by day 27, except around the bill and the tail feathers. Nestlings gained mass (x ± SD) at a rate of 1.5 ± 0.1 g/day (n = 3) during the first 17 days, reaching a mass of 30.45 g (Fig. 2A).
FIG. 1. Incubation patterns of the Fulvous-breasted Flatbill during 24 hrs and different days in two nests: (A) day 7, (B) day 12, and (C) day 24 of incubation of the first nest, and (D) last day of the incubation period of the second nest.

Nestling mass decreased to 27.85 g after day 17, where it remained until the last measurement (day 29), when the nestling was completely covered with feathers and active. Recently hatched nestlings (day 1) had a tarsus length of 8 mm and a wing length of 7 mm ($n = 3$), and grew at a rate of 0.7 and 2.9 mm/day, respectively, reaching a length of 22 and 64 mm on day 29.

The average body temperature of nestlings during the first 16 days was 31.6°C (27.88–33.63°C), and body temperature decreased 4.08°C in 3 min after nestlings were removed from the nest. The change in body temperature at day 17 was smaller (between 1 and 2°C) and, for the last 2 days (28 and 29), the nestling was able to regulate its body temperature at 37.34°C (Fig. 2B). We left the sensor in one nest after one of the eggs hatched, and quantified 29 trips/day, which is 14 trips higher than the maximum number during incubation. The presumed female had short incubation bouts (<7 min) and variable foraging bouts between 10 and 45 min after hatching of young.

We conducted direct provisioning observations at the first nest when the nestlings were 4 and 7 days age from 1645 to 1745 and 0837 to 0937 hrs, respectively. We only observed one parent visiting the nest per provisioning trip, but cannot be sure that only one parent fed the nestlings. The parent made four and three trips/hr, respectively, and stayed inside the nest for 5 min on average during each provisioning trip. We could not document the prey type brought by the parent to the nest or where the parent was foraging.

DISCUSSION

The eggs and nests in our study were similar to those previously reported for this species (Greeney et al. 2004, Brumfield and Maillard 2007). The incubation period was long compared to other neotropical passerine birds (Tieleman et al. 2004; Auer et al. 2007; Martin et al. 2007;
Nestling development and body temperature in two nests of the Fulvous-breasted Flatbill. (A) Mass increments of three nestlings from two different nests. The circles and triangles correspond to two nestlings from the first nest and the square corresponds to the single nestling from the second nest. (B) Daily nestling temperature loss throughout the nestling period after exposing nestlings to environmental temperature for 3 min. Symbols are the same as in A.

GAL, unpubl. data), and 6 days longer than the partial period reported for this species by Greeney et al. (2004). The nestling period was also long but similar to the 27 days reported by Greeney et al. (2004). Nest location was also similar to previous studies: over small creeks inside the forest and attached to branches and epiphytes between 3 and 12 m high (Parker and Parker 1982, Greeney et al. 2004, Brumfield and Maillard 2007). Nest materials, location, and shape are similar among Rhynchocyclus species (Fitzpatrick et al. 2004); those described for the sister group (Tohomyias spp.) were classified as a closed/retort/pensile structure with a vertical/downward tube (Simón and Pacheco 2005).

The clutch size in our study is consistent with that previously reported for R. fulvipes and other species of this genus (1-3 eggs; Parker and Parker 1982, Fitzpatrick et al. 2004, Greeney et al. 2004, Brumfield and Maillard 2007). Nestling body mass when fully feathered was 4 g higher than the reported adult mass (23.1 g) (Dunning 2008).

The nestling was able to regulate body temperature after it was fully feathered, but this
temperature (37°C) was lower than average bird body temperature (40°C) (Gill 2007). Dunn (1975) suggested that altricial nestlings became endothermic when nesting body mass was 60–70% of their parents body mass. However, Ricklefs and Hainsworth (1968) suggested endothermy in nesting birds is not influenced by body mass. They suggested endothermy is proportional to the length of the nestling period, where nestlings of species with shorter nestling periods will become endothermic faster than species with longer nestling periods. Our study suggests thermoregulation occurs when the feathers are completely developed. However, further studies of other species are necessary to evaluate if endothermy correlates with completion of feather development.

Nest attentiveness was 64%, which is similar to other neotropical passerine species (Tieleman et al. 2004, Auer et al. 2007, Martin et al. 2007). However, unlike previously documented increases in nest attentiveness throughout the incubation period in neotropical passerines (Martin et al. 2007, Londino 2009), R. fulvipes decreased time on the nest as incubation period progressed. This reduction resulted from a small change in the number of trips (17%). Time on the nest decreased a few days prior to egg hatching for both nests, but the behavior used by the two individuals to decrease time on the nest differed. The female at the first nest increased the number of trips, but the female at the second nest increased length of foraging bouts. This suggests tropical birds have multiple ways to regulate egg temperature during incubation to successfully reach egg hatching within and between species. Intrinsic factors may have an important role on behavioral decisions during incubation.

Our study reinforces the specificity of the genus Rynchocyclus for nesting sites along creeks, and indicates R. fulvipes has longer incubation and nestling periods compared to other tropical species (Tieleman 2004, Auer et al. 2007, Martin et al. 2007).

ACKNOWLEDGMENTS

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ABSTRACT.—Temporal aspects of egg deposition are important factors governing avian reproductive success. I report hourly egg-laying patterns of the Pearly-eyed Thrasher (Margarops fuscatus) in the Luquillo Experimental Forest in northeastern Puerto Rico during 1979–2000. Initiatory eggs were laid by early morning (median = 0642 hrs. AST) and almost half of the eggs were laid by 0723 hrs. Many penultimate eggs completing a clutch, however, were laid later in the morning and some not until mid afternoon (1429 hrs), thus extending egg deposition by 8 hrs. Delayed laying of the last eggs in a clutch may be an adaptive strategy triggering brood reduction to ensure survival of older and more robust siblings during periods of physiological stress and food shortages. There is substantial variation in the precise hour of egg laying in birds (Scott 1991, McMaster et al. 2004), but most birds generally lay their eggs in the morning. Many north-temperate passerines lay one egg per day, often within 2–3 hrs shortly before or after local sunrise until the clutch is complete (Skutch 1952, Brackbill 1958, Nolan 1978, Scott 1993, Haftorn 1996, McMaster et al. 2004). Temporal aspects of egg deposition affect all aspects of avian reproduction, e.g., egg size, hatching patterns and synchrony, size, fitness, and viability of nestlings (Williams 1994, Maddox and Weatherhead 2008). Egg size, usually expressed in volumetric or longitudinal measures (Barta and Szekely 1997), is often correlated to hatching size, fitness, and subsequent nestling development (Slagsvold et al. 1984, Deeming and Birchard 2007). However, Ricklefs (1984) cautioned using egg size or mass as a measure of egg quality as actual composition, e.g., the amount and quality of yolk, is usually independent of linear or volumetric measures. Even variation in embryonic metabolic rates influences time of hatching and hatching size, and maturation and fitness (Badzinski et al. 2002). Maddox and Weatherhead (2008) suggested that other maternal factors, e.g., asynchronous hatching, override many of the previously espoused endogenous and environmental factors.

Knowledge of timing of laying appears to not have been reported for the Pearly-eyed Thrasher (Margarops fuscatus). The objective of this paper is to report the chronology and pattern of egg deposition for a montane population in Puerto Rico and relate it to the asynchronous hatching observed in this population.

METHODS

The study area was within the 11,330-ha Luquillo Experimental Forest (LEF) in eastern Puerto Rico.
TABLE I. Number of nest visits for the egg of the day. The proportion of nests containing a new egg changed from <50 to >50% by 0829 hrs (bold).

<table>
<thead>
<tr>
<th>Hrs</th>
<th>Nest visits</th>
<th>Egg of the day</th>
<th></th>
<th>Proportion</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>0600-0629</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0/3</td>
<td>0</td>
</tr>
<tr>
<td>0630-0729</td>
<td>27</td>
<td>12</td>
<td>15</td>
<td>12/27</td>
<td>44%</td>
</tr>
<tr>
<td>0730-0829</td>
<td>85</td>
<td>63</td>
<td>20</td>
<td>63/83</td>
<td>76%</td>
</tr>
<tr>
<td>0830-0929</td>
<td>132</td>
<td>110</td>
<td>24</td>
<td>110/134</td>
<td>82%</td>
</tr>
<tr>
<td>0930-1029</td>
<td>181</td>
<td>163</td>
<td>18</td>
<td>163/181</td>
<td>90%</td>
</tr>
<tr>
<td>1030-1129</td>
<td>228</td>
<td>222</td>
<td>6</td>
<td>222/228</td>
<td>97%</td>
</tr>
<tr>
<td>1130-1229</td>
<td>160</td>
<td>156</td>
<td>4</td>
<td>156/160</td>
<td>98%</td>
</tr>
<tr>
<td>1230-1329</td>
<td>85</td>
<td>82</td>
<td>3</td>
<td>82/85</td>
<td>96%</td>
</tr>
<tr>
<td>1330-1429</td>
<td>56</td>
<td>54</td>
<td>2</td>
<td>54/56</td>
<td>96%</td>
</tr>
<tr>
<td>1430-1529</td>
<td>34</td>
<td>34</td>
<td>0</td>
<td>34/34</td>
<td>100%</td>
</tr>
</tbody>
</table>

*Two time periods between which the increase in the proportion of EODs (egg of the day) was significant (z-test for rates and proportions using Yates correction).

RESULTS

One egg was laid each day until the clutch was complete (n = 1,089 observations during 1979-2000). Most eggs were laid in the morning (0630-1129 hrs; median lay hour = 0723). Forty-four percent were laid by 0729 hrs and 76% were laid by 0829 hrs. However, the latter eggs (2nd, 3rd, 4th eggs in 2-, 3-, and 4-egg clutches) are laid later in the day, and all EODs were not found in the nest until 1529 hrs (Table 1).

The first two eggs of a clutch were generally laid by mid morning (0630-0929 hrs), whereas the last egg (usually the third, and much less frequently a fourth) was often laid later in the day (until 1429 hrs) and was responsible for expansion of the hourly laying period (Fig. 1). Almost 90% of the eggs initiating a clutch were laid by 0729 hrs, and most were present by 0829 hrs (median = 0642 hrs). Second-laid eggs were not always laid in the early morning or afternoon as they were laid in the early morning or afternoon as they were laid in the late afternoon. Almost 90% of the eggs initiating a clutch were laid by 0729 hrs, and most were present by 0829 hrs (median = 0642 hrs). Second-laid eggs were not always laid in the early morning hours as they were initial eggs of a clutch because second-laid eggs in 151 nests completing the clutch some were laid as late as 1529 hrs. Only about half of second-laid eggs were present by 0729 hrs (median = 0713), whereas most (68%) were not present until 0929 hrs. All second-laid eggs were present well after mid-day (1529 hrs at the latest) (Fig. 1). Most third-laid eggs were laid between 0729 and 0829 hrs (median = 0826) when 39% were present, and 74% were present by 1029 hrs. All third-laid eggs were present by 1529 hrs. None of the 22 fourth-laid eggs was present until between 0830 and 0929 hrs (median = 0957) when 25% were recorded. All fourth-laid eggs were present by 1029 hrs (Fig. 1). There was no significant trend for day of the week initiatory eggs were laid, although there was a continuous increase each day from Sunday to Friday, with prominent increases from Sunday to Monday and Thursday to Friday (Fig. 2).
FIG. 1. Hourly egg-laying patterns by lay order for Pearly-eyed Thrashers in the Luquillo Experimental Forest, Puerto Rico (Dec 1979–Jul 2000). Sample sizes for the four categories: first-laid (343), second-laid (401), third-laid (323), and fourth-laid (22). Arrows indicate when the proportion of EODs (egg of the day) present was greater ($z = 0.05$) than within the previous hourly range.

FIG. 2. Number of clutches initiated each day of the week. There was an increase from the first to the penultimate, but a precipitous decline on the last day.
DISCUSSION

The median hour of egg deposition for the Pearly-eyed Thrasher population studied was 0723 hrs, which is similar to the median hour of laying (0700 hrs) calculated for the Gray Catbird (Dumetella carolinensis) (Scott 1993). Official sunrise in Puerto Rico varies 73 min (0547 to 0700 hrs; median = 0613 hrs) throughout the year (U. S. Department of Commerce 2011). The Pearly-eyed Thrasher has an extended laying period, laying most of its eggs by 1129 hrs, or ~5 hrs and 7 min after local sunrise, and can delay deposition until at least 1429 hrs. This pattern is similar to its close relative, the European Starling (Sturnus vulgaris), which also has close phylogenetic affinities with the Gray Catbird (Meijer 1992:fig. 2; Ericson and Johansson 2003:fig. 1). Other members of the superfamily Muscicapoidae, e.g., thrushes and flycatchers, are also known to lay in the afternoon (Brackbill 1958, Weatherhead et al. 1991). Oppenheimer et al. (1996) reported that much of the variation in laying times reflects phylogeny, which is reflected in the pattern recorded for the Pearly-eyed Thrasher.

The initial egg mass at laying for most birds is an important factor affecting hatching mass (Deeming and Birchard 2007). The first two eggs in the laying sequence of the Pearly-eyed Thrasher are heavier and are laid earlier in the day than the last one or two eggs completing the clutch (Arendt 2006). Initial eggs of a clutch laid early in the day contribute to a greater age gap between older and younger siblings, giving older siblings developmental and survival advantages over younger nest mates during periods when food and other resources may be critically limited (Esler 1999, Maddox and Weatherhead 2008). First- and second-hatched Pearly-eyed Thrasher fledglings had a higher probability of being recruited into the breeding population and dispersed earlier and farther than younger siblings (Arendt 2006). First- and second-hatched thrasher fledglings, heavily parasitized by philornis (Philornis spp.) botfly larvae (Diptera: Muscidae), lived significantly longer and survived better than younger siblings with comparable larval numbers (Arendt 1985, 2000). Unparasitized third- and fourth-hatched siblings would often fledge at similar body masses and appendicular measurements as those of older siblings but, during food shortages, many would lag in development, eventually becoming runts. They would be trampled to death by older siblings, or simply disappear from nests. I observed females on several occasions carrying runt nestlings and discarding them 20–30 m from their nest boxes (Arendt 2006). Delayed laying in the LEF population of the Pearly-eyed Thrasher of the final eggs of a clutch may be an adaptive strategy triggering brood reduction to ensure survival of older, more robust siblings during periods of physiological and environmental stress, e.g., food shortages (Knight 1987, Murray 1994, Maddox and Weatherhead 2008).

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I appreciate the assistance of my wife Angela I. Arendt, parrot project volunteers, and my staff: G. Cabán Ruiz, Carlos Cianchini Oscar Díaz, Roberto Díaz and M. R. Ford. This research was done in cooperation with the University of Puerto Rico.

LITERATURE CITED


SHORT COMMUNICATIONS 627


First Record of Interspecific Breeding of Least Bell's Vireo and White-eyed Vireo

Melissa A. Blundell1,2,3 and Barbara E. Kus1

ABSTRACT.—We provide the first known documentation of a male Least Bell's Vireo (Vireo bellii pusillus) breeding with a female White-eyed Vireo (V. griseus) and the first report of a White-eyed Vireo breeding in California at the San Luis Key River, Oceanside, San Diego County. We discovered the pair building a nest on 12 May 2010. The female laid four eggs, and the pair successfully raised and fledged four nestlings. We collected DNA samples from each nestling and the female during the nestling stage and banded them with a numbered federal leg band for future identification. We obtained detailed nest measurements after fledging and monitored the territory for further nesting attempts. No additional nesting attempts were detected. Received 29 November 2010. Accepted 29 March 2011.

The Least Bell's Vireo (Vireo bellii pusillus) is a federally endangered migratory songbird that breeds from southern California, USA to northern Baja California, Mexico between late March and mid-August (Kus et al. 2010) with the majority of the population breeding in San Diego County along the San Luis Rey and Santa Margarita rivers. The White-eyed Vireo (V. griseus) is a migratory songbird that primarily breeds in eastern North America (from southern Florida to southeast Massachusetts and west through Illinois) and into central North America (from
eastern Iowa to west-central Texas and northeastern Mexico) between early April and early August (Hopp et al. 1995). White-eyed Vireos are rare vagrants in California, with 67 confirmed sightings statewide between 1969 and 2009, only eight of which occurred in San Diego County (California Bird Records Committee 2007, 2010). Five of the San Diego County sightings were during the breeding season, while three were fall migrants (1 Sep–30 Oct). We report the first known documentation of a Least Bell's Vireo, one of four subspecies of Bell's Vireo (V. bellii), breeding with a White-eyed Vireo. This is the first documented case of a White-eyed Vireo breeding in California and appears to be the first successful nesting of a mixed pair of any two vireo species observed in the field.

OBSERVATIONS

We observed a male Least Bell's Vireo breeding with a female White-eyed Vireo at the San Luis Rey River, Oceanside, San Diego County, California (33°13.86' N, 117°20.68' W). One observer (MAB) observed a male Least Bell’s Vireo building a nest with a female White-eyed Vireo on 12 May 2010 (Fig. 1). The pair likely had just started building the nest, as it was ~10% complete and consisted of a woven hammock attached to the branch of an arroyo willow (Salix lasiolepis). The following day (13 May), the nest was 60–70% complete with a strong cup formation. The Least Bell’s Vireo was identified as male as he sang on the nest. Two additional observers corroborated identification of the female as a White-eyed Vireo on the same day. Six days later (19 May) and 12 days later (25 May), two and four eggs, respectively, were observed in the nest. The presence of eggs corroborated the White-eyed Vireo was female. The male was incubating the eggs during these two visits. The nest was still active on 1 June with four eggs and the female was incubating the clutch. Four days later (5 Jun), four nestlings ranging from 1 to 2 days of age were present, placing 3 June as the approximate hatch date.

We banded the four nestlings (5–6.5 days of age) on 9 June with single anodized aluminum dark blue numbered federal bands. We used a mist net during the same visit to catch the female White-eyed Vireo as she approached the nest. We
TABLE 1. Nest dimensions of Least Bell’s Vireo, White-eyed Vireo, and a mixed species pair.

<table>
<thead>
<tr>
<th></th>
<th>Mixed pair</th>
<th>Least Bell’s Vireo</th>
<th>White-eyed Vireo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest height, m(h)</td>
<td>0.86</td>
<td>1.00 ± 0.40</td>
<td>0.94 ± 0.13</td>
</tr>
<tr>
<td>Inside diameter, mm(d)</td>
<td>46</td>
<td>49.9 ± 5.1</td>
<td>50.5 ± 4.6</td>
</tr>
<tr>
<td>Nest depth, mm(e)</td>
<td>52</td>
<td>46.7 ± 5.4</td>
<td>53.7 ± 4.5</td>
</tr>
<tr>
<td>Cup height, mm(f)</td>
<td>85</td>
<td>62.1 ± 9.5*</td>
<td>97.2 ± 10.9</td>
</tr>
</tbody>
</table>

*a* Unpublished data from this study for the San Luis Rey River, California.  
*b* Hopp et al. 1995.  
*c* Distance from ground to top rim of nest.  
*d* At widest point measured inside the rim.  
*e* Distance of lowest rim to bottom of inside of nest.  
*f* Highest rim of the nest to outside bottom of the nest.  
\(^{9}\) Arizona subspecies \(V. b. arilome\).  
\(^{10}\) Kus et al. (2010). Harrison (1979) provides an average range of 71-98 mm.

did not attempt to catch the male Least Bell’s Vireo to minimize disturbance. We banded the White-eyed Vireo with a single aluminum numbered federal band. We annually conduct intensive band observations for Least Bell’s Vireos throughout southern California and should be able to detect these individuals if they return in future years. We also collected DNA samples from each individual. We collected a pin feather sample from each nesting and a blood sample from the female via a toenail clip. This genetic material is currently being analyzed for further evidence of this interspecific breeding occurrence.

The nest was empty on 14 June and two fledglings were heard calling nearby. Three more visits were made to the territory to search for a second nesting attempt, but none was detected, nor was the female White-eyed Vireo observed. One individual (MAB) observed one of the banded fledglings with the male Least Bell’s Vireo on 27 June. The fledgling resembled a Least Bell’s Vireo fledgling in appearance with a white underbelly, gray crown, back and primaries, and black eyes.

The pair’s pendile nest was suspended in an arroyo willow from the crook of a Y-shaped horizontal branch. We obtained nest dimensions (Table 1) for comparison with average measurements for nests of Least Bell’s Vireo and White-eyed Vireo. The nest was left undisturbed in the territory.

**DISCUSSION**

Interspecific breeding among vireos is rare. A Blue-headed Vireo \((V. solitarius)\) and Yellow-throated Vireo \((V. flavigrns)\) hybrid has been recorded (James 1998). Additionally, Hauser (1959) provides documentation of a female Blue-headed Vireo and male Yellow-throated Vireo constructing a nest together, although the nest was not used. Additional hybrids have been implicated through genetic analysis or physical characteristics (McCarthy 2006, Chartier 2008), but documentation in the field of successful nesting of any two vireo species is lacking prior to our observations.

A comparison of cytochrome b sequences using gel electrophoresis showed Bell’s Vireo and White-eyed Vireo to be sister taxa and more closely related to each other than to any other vireo species analyzed (Murray et al. 1994). Least Bell’s Vireos and White-eyed Vireos share similar breeding behaviors that may have facilitated this pairing and successful production of young. Least Bell’s Vireos typically breed in dense, low, early successional vegetation (Kus et al. 2010), and White-eyed Vireos are common in low trees and shrubs, dense secondary deciduous scrub, wood margins, and overgrown pastures (Hopp et al. 1995). Both male and female Least Bell’s Vireos and White-eyed Vireos participate in nest-building, incubation, and parental care.

Least Bell’s Vireos typically lay three to four eggs per clutch, incubate for ~14 days, and fledge young ~10-12 days later (Kus et al. 2010). White-eyed Vireos typically lay four eggs per clutch, incubate for ~14 days, and fledge young 9-11 days later (Hopp et al. 1995). Harrison (1979) notes that Bell’s Vireo nests are indistinguishable from White-eyed Vireo nests, while Kus et al. (2010) suggest Bell’s Vireo nests may be smaller, more finely constructed, and have a shorter outside height than White-eyed Vireo nests. The height of the mixed pair’s nest was within the average range for those recorded for Least Bell’s Vireo and White-eyed Vireos.
Inside nest diameter was close to average for Least Bell's Vireos and at the low end of the range for White-eyed Vireos. Nest depth and cup height were greater than average for Least Bell's Vireos but near average for White-eyed Vireos. This may indicate that females affect these nest parameters during nest building. Alternatively, since White-eyed Vireos are on average larger (female: 11.7 g, range = 10.5-13 g, n = 6; Hopp et al. 1995) than Least Bell's Vireos (combined sex: 8.5 g, range = 7.4-9.8 g, n = 33; Kus et al. 2010), the nest depth and cup height may be a reflection of the female's size rather than any sex-specific influence on nest dimensions.

Hopp et al. (1995) reported that upon fledging, young White-eyed Vireos appear similar in plumage coloration to adults, but are less yellow. They also note the iris is brownish in White-eyed Vireos up until November of the hatching year, Pyle (1997) notes that hatch-year and second-year birds display a brownish-gray to grayish iris through February and after-hatch-year birds usually display a white or white with slight grayish wash iris (Aug-Jul). It will be interesting to see what combination of Least Bell's Vireo and White-eyed Vireo morphological characteristics are expressed in the adult plumage should the hybrid young return to the study area in future years. It will also be interesting to see if they attempt to breed and are successful.

Least Bell's Vireos and White-eyed Vireos differ greatly in plumage and song. Least Bell's Vireos appear nearly entirely gray with two wing bars and white on the chest, sides, belly, and flanks, and have a black iris (Kus et al. 2010). White-eyed Vireos have a more distinct facial pattern (yellow lores, white iris), yellow sides and flanks, two bold wing bars, white throat and belly, and greenish-gray to olive green upperparts (Hopp et al. 1995). Both are sexually monomorphic. The Least Bell's Vireo primary song consists of a rapid sequence of short, distinctive notes that progressively increase in amplitude. Each song has a raspy or jumbled quality and songs are delivered as alternating pairs (Kus et al. 2010). The White-eyed Vireo song begins and ends with a short chip note, and consists of a series of rapid and complex whistle notes, tick notes, and buzzes (Bradley 1980). Differences in plumage and song were not barriers to courtship and pairing in this interspecific mating, despite their importance as cues in species recognition and mate selection in songbirds (e.g., Marler 1960, Lack 1968). The female White-eyed Vireo was in a situation in which there were no potential conspecific mates which may have changed her threshold(s) of responsiveness to cues in the environment.

ACKNOWLEDGMENTS

We thank Lisa D. Allen for photography/video documentation and Kimberly Ferree for corroborating the sighting. We also thank Suellen Lynn, Kathleen Longshore, Roger L. Hostem, and two anonymous reviewers for helpful comments on the manuscript. Funding was provided by the U.S. Army Corps of Engineers, Los Angeles District. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Triorchidism in a Hummingbird

Christopher C. Witt\textsuperscript{1,3} and Emil Bautista\textsuperscript{2}

ABSTRACT.—We report a Great-billed Hermit (Phaethornis malaris) with three testes, a condition known as triorchidism. This is the first case to our knowledge of triorchidism in Neoavcs, the clade that contains ~95% of avian species diversity. Triorchidism is inferred to be an exceptionally rare congenital abnormality in wild birds with developmental cause and evolutionary implications that are distinct from testicular asymmetry. Received 16 November 2010. Accepted 21 March 2011.

Triorchidism is the condition of having three testes. This and other forms of polyorchidism are associated with superfecundity, 'amorous propensities,' and 'generative faculties' in mythology (Gould and Pyle 1896). The true pathology is poorly known due to a paucity of cases and is dependent on the underlying developmental cause (Leung 1988). Several instances of triorchidism have been reported in Domestic Chickens (Gallus gallus) (Katiyar et al. 1986, Shravastava et al. 1988, Hocking 1992) and in a captive-bred line of Japanese Quail (Coturnix japonica) (McFarland 1965), but the phenomenon of polyorchidism is otherwise scarcely known from non-human animals.

Triorchidism is typically thought to comprise a congenital developmental abnormality and is associated with normal histology and functional spermatogenesis in the third testis in more than half of human cases (Ozok et al. 1992, Spranger et al. 2002, Savas et al. 2009). It is distinct from testicular asymmetry, which is widespread in birds and has been found to correlate with age (Graves 2004) or secondary sexual characteristics (Möller 1994; but see Kimball et al. 1997). The phylogenetic distribution of triorchidism in vertebrates is poorly known due to a scarcity of reports. We describe a case of triorchidism in the Great-billed Hermit (Phaethornis malaris) from the humid lowland forests of northeastern Peru, and review previous reports of triorchidism in birds.

METHODS

We conducted a site inventory during June 2007 in the Rio Chipaota Valley, Department of San Martín, Peru, while concurrently collecting comparative data on bird physiology (Merkord et al. 2009). This work included collection of voucher specimens with detailed ancillary data for deposit in the collections of Centro de Ornitología y Biodiversidad (CORBIDI, Lima, Peru) and the University of New Mexico, Museum of Southwestern Biology (MSB, Albuquerque, New Mexico, USA). We collected the following data for all specimens using standard methods: (1) body mass, (2) hemoglobin concentration (using Hemocue 201+ with correction for avian blood, following Simmons and Lill 2006), (3) hematocrit, (4) red blood cell concentration, (5) presence of hematozoon in a Giemsa-stained blood smear, (6) skull ossification, (7) presence and dimensions of the bursa of Fabricius, and (8) identity, condition, and dimensions of gonads.

OBSERVATIONS

We captured a specimen of Great-billed Hermit on 15 June 2007 that proved upon autopsy to have an anomalous third testis (Fig. 1). The left testis appeared to be divided into two similarly sized, spherical testes (left-most testis 2.87 mm diam, center testis 3.41 mm diam), connected to a single ductus deferens. The right testis was slightly smaller in size (2.65 mm diam) and appeared to be displaced posteriorly by the two left testes, which together occupied a substantial portion of the abdominal cavity. We lacked the ability to do histological examination in our remote field camp, but we suspect that all three testes were functional because they were similar in size and
nearly indistinguishable in shape, color, firmness, and internal consistency and appearance.

The triorchid Great-billed Hermit was netted in mature forest interior habitat, at 374 m asl, 06°38.660' S, 76°04.955' W ± 10 m. It lacked a bursa of Fabricius, and the skull was estimated to be 30% ossified, an exceptionally high ossification for a hummingbird and a strong indication that the bird was reproductively mature. The voucher specimen and frozen tissue are archived at MSB (Tissue catalog number NK162363, voucher number EBO247) with a duplicate tissue sample archived at CORBIDI. The bird was physiologically normal based on comparison to

**DISCUSSION**

This represents the first reported case of triorchidism for a hummingbird (Trochilidae) and for the entire clade Neoaves, which includes
~95% of avian species diversity. We can find no previous reports of this phenomenon in wild bird species, nor any bird species outside of the Order Galliformes. Triorchidism in birds was first reported by McFarland (1965), who examined >2,000 male Japanese Quail and found one case of triorchidism that was associated with absence of the right kidney. In that case, the right testis was divided into two nearly co-equal sections, both of which were undergoing normal spermatogenesis. Katiyar et al. (1986) first reported a supernumerary right testis in a Domestic Chicken. Shrivastava et al. (1988) subsequently reported a Domestic Chicken with a supernumerary left testis that was severely reduced in size (less than 10% the size of the left and right testes) and ~1 cm posterior to the caudal end of the left testis, ventral to the third lobe of the left kidney. The small round supernumerary testis was softer in consistency, and normal in color and spermatogenic activity by histological examination.

Hocking (1992) systematically examined the testes of 378 male Domestic Chickens and found three cases of triorchidism, each of which was comprised of two left testes. The two left testes in two of the three cases were nearly co-equal in size with normal semen quality and testis histology. The smaller of the two left testes in the third case was much less than half the volume of the larger one and was characterized by strongly reduced spermatogenesis. Hocking (1992) suggests that supernumerary testes probably originate by congenital defect and are fairly common in domestic fowl, as indicated by his finding prominent third testes in 0.8% of males. Supernumerary testes originating by congenital defect should be present throughout life, in contrast to asymmetrical testes, which are known to shift in relative size according to age, season, overall condition, and other, unidentified factors (Moller 1994, Kimball et al. 1997, Graves 2004).

We examined and measured testes in 591 male hummingbirds representing 65 species during fieldwork between 2006 and 2010, including 21 male Great-billed Hermits (MSB and CORBIDI specimen data). We observed only one case of triorchidism (0.17% of male hummingbirds examined), suggesting the phenomenon is significantly less common in wild hummingbirds than in domestic fowl, although the small sample size of triorchid individuals prohibits statistical testing.

The paucity of case reports of supernumerary testes in birds makes it difficult to understand the mechanisms or risk factors that may be associated with this condition. However, ~100 cases of triorchidism in humans have been described (Hassan et al. 2008), and the developmental, pathological, and functional aspects of human triorchidism are useful for understanding avian triorchidism. Approximately two-thirds of human supernumerary testes occurred on the left side as in the triorchid hummingbird, and a slightly smaller proportion (63%) have reproductive potential as evidenced by normal spermatogenesis (Spranger et al. 2002, Bergholz and Wenke 2009). Leung (1988) classified cases of polyorchidism into four types, of which the triorchid hummingbird seems to fit into "type C", which is characterized by the supernumerary testis having its own epididymis and sharing the ductus deferens with the regular testis in a parallel fashion. This configuration is thought to occur due to incomplete longitudinal division of the genital ridge and the proximal portion of the mesonephric duct during development (Singer et al. 1992).

Two cases of triorchidism have been observed in a rare Malagasy tortoise, Geochelone yniphora (Mourgue 1989), suggesting the phenomenon occurs in at least three deep amniote lineages. The present case is the first report for a wild bird and the first for any bird outside of the Order Galliformes. The hummingbird species involved, the Great-billed Hermit, is a promiscuous, lek mating species and is expected to be under selection for sperm volume and quality (Birkhead 1998). It is not known whether this evolutionary pressure may be associated with susceptibility to presumed congenital defects such as the supernumerary testis observed. Investigators performing autopsies on birds should look for and report supernumerary testes to help elucidate the phylogenetic distribution and evolutionary implications of this interesting phenomenon.

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LITERATURE CITED


Nest Reuse by the Scintillant Hummingbird (Selasphorus scintilla)

Emilia Triana¹ and Luis Sandoval¹,²,³

ABSTRACT.—Nest reuse behavior in birds is rare because nests are ephemeral structures. We describe the first record of multi-season nest reuse by the Scintillant Hummingbird (Selasphorus scintilla). The nest was a multi-cup of four nests with newer nests placed on top of older nests. The nest was under the eave of a roof, which may have reduced nest disintegration and facilitated nest reuse. Received 19 November 2010. Accepted 19 March 2011.

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Reuse of nests is an uncommon behavior by birds mainly because the nest structure remains intact only for a short period of time after the bird leaves the breeding area (Skutch 1976, Bertolero 2002). except for cavities (e.g., wood, termitaria, and earth) that persist (Aitken et al. 2002, Sandoval and Barrantes 2009). The vegetal material of a nest and weather conditions, such as rainfall and wind, disintegrate the nest rapidly and prevent successive use, even in the same season if time between nest attempts is lengthy (Aguilar and Marini 2007). Another factor that may prevent or reduce nest reuse is persistence of parasites in old nesting material. Parasites feed on nestlings when the nest is reused, resulting in reduced reproductive success (Moss and Camin 1970, Barclay 1988, Rendell and Verbeek 1996).
Notable examples of nest reuse occur in raptors (Falconiformes, Accipitriformes) and storks (Ciconiidae). Many species from these groups can reuse the same nest in successive years and even add new material each year, which increases nest size (Dijak et al. 1990, Cezilly et al. 2000, Vergara et al. 2006, Stout et al. 2007). Nest reuse by hummingbirds has been reported previously (Skutch 1973), but only in North American species (Gault 1885, Baltosser and Scott 1996, Baltosser and Russell 2000). We provide another example of nest reuse behavior with the first report of a multi-season nest reuse by the Scintillant Hummingbird (*Selasphorus scintilla*). This hummingbird is a common endemic of Costa Rica and west Panama, occurring between 900 and 2,100 m asl. Nests of this species are usually in bushes at forest borders or in open areas (Stiles and Skutch 1989).

**OBSERVATIONS**

We found an empty Scintillant Hummingbird nest at La Colmena, Vásquez de Coronado, San José Province, Costa Rica (09° 59' N, 83° 59' W; 1,500 m asl) on 15 March 2010. The site borders a small secondary forest patch between farm fields and isolated houses.

The nest was a multi-cup structure (Fig. 1) attached from the bottom to the base of a light bulb 2.5 m above ground on a residential porch. The nest was comprised of four similar nest cups with newer nests on top of the older ones. The outer layer of the four individual nests consisted of mosses, lichens, and spider webs. The inner layer was composed mainly of Asteraceae seeds. These characteristics are in agreement with previous nest descriptions of Scintillant Hummingbirds (Stiles and Skutch 1989). There was little variation between the diameters of the nest cups (CV = 16%), in comparison to variation found in nest height and depth of the egg chamber (CV = 145 and 87%, respectively, Table 1).

The size of the egg chamber could be an indicator of nest success. Hummingbird hatchlings grow inside their nests and the egg chamber increases in size. The egg chamber in the fourth and newest nest was wider than the other three (Fig. 1, Table 1); we assume this was the only nest where eggs apparently hatched, because when nestlings grow they expand the egg chamber. An entire egg shell broken in two pieces.

### TABLE 1

<table>
<thead>
<tr>
<th>Nest</th>
<th>Diameter</th>
<th>Egg chamber depth</th>
<th>Nest height</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>19.2 × 22.5</td>
<td>17.8</td>
<td>43.2</td>
</tr>
<tr>
<td>2</td>
<td>20.0 × 22.7</td>
<td>21.1</td>
<td>35.8</td>
</tr>
<tr>
<td>3</td>
<td>19.2 × 22.1</td>
<td>14.5</td>
<td>26.0</td>
</tr>
<tr>
<td>4</td>
<td>21.6 × 24.5</td>
<td>24.0</td>
<td>37.9</td>
</tr>
</tbody>
</table>
from a previous nesting attempt was within the second egg chamber (Fig. 1), which suggests, at least in this nest, that two eggs may have been laid. We found no evidence of egg shells inside the other two nest cups and their size was smaller than the fourth. The nests were collected and deposited in Museo de Zoología, Universidad de Costa Rica.

DISCUSSION

Nest reuse in birds could be related to nesting success, nest site fidelity, or habitat limitation (Harvey et al. 1979, Vergara et al. 2006, Aguilar and Marini 2007). The first two causes would be more likely if previous nesting attempts were successful (Beheler et al. 2003, Hoover 2003). Nest choice in hummingbirds and other species that nest during the rainy season, such as the Scintillant Hummingbird (Stiles and Skutch 1989), may be limited to locations with adequate nest cover. Nests with better shelter from the environmental elements (e.g., less direct rain) may reduce thermoregulatory costs (Calder 1971). Sheltered nests may allow the female to spend more time foraging, because eggs and chicks are relatively protected. The Scintillant Hummingbird nest that we observed was completely sheltered and the benefits of shelter may be the main reason this nest was reused on multiple occasions. Also, if the light bulb was on during part of the day, it might have reduced thermoregulatory costs.

We do not know if all nest attempts were successful, but our data suggest the only successful nest was the fourth. We based this upon it having a larger egg chamber size, a characteristic observed in several hatching hummingbird nests (Calder 1973, Baltosser 1986). It is possible that nesting success was not the main cause of nest reuse. Most hummingbird females are territorial against conspecifics (Stiles and Skutch 1989), which suggests the nest was built by only one female, as occurs for Costa’s (Calypte costae) and Black-chinned (Archilochus alexandri) hummingbirds (Gault 1885, Baltosser and Scott 1996, Baltosser and Russell 2000). However, we are not certain if all nests were built by the same female, in which case nesting success may have nothing to do with the nest reuse.

Nest reuse may have also occurred because it was structurally solid, and was a good foundation for a second nest (Bergin 1997). Generally, this condition is rare in the tropics, where decomposition rate for vegetal material is high (Sandoval and Barrantes 2009). We believe the reuse of this Scintillant Hummingbird nest was most likely due to the ideal nest location below a covered structure.

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LITERATURE CITED


Harvey, P. H., P. J. Greenwood, and C. M. Perrins.
 Natal and Adult Dispersal of Red-eyed Vireos in a Large Southern Ontario Forest

Benjamin J. Walters\textsuperscript{1,2} and Erica Nol\textsuperscript{1}

ABSTRACT.—We report re-encounter rates and dispersal distances of Red-eyed Vireos (\textit{Vireo olivaceus}) re-encountered 1 year after banding in a large forest (~4,600 ha) in southern Ontario, Canada. We re-encountered 12 (11%) of 109 banded individuals. Dispersal distances ranged from 40 to 9,870 m and were longest for hatch year (HY) bandings (median = 4,970 m, \(n = 3\)). Distances were similar between other age classes (SY: median = 225 m, \(n = 4\); ASY: median = 220 m, \(n = 5\)), and males (median = 220 m, \(n = 9\)) and females (median = 250 m, \(n = 3\)). Our re-encounters of banded Red-eyed Vireos provide information on dispersal, detection rates, and methodology that could potentially improve future marking efforts and apparent survivorship estimates. Re-encounters of marked birds provide measures of annual survivorship needed to assess population viability (Gould and Nichols 1998), population change (Anders and Marshall 2005), fecundity (Anders et al. 1997), and fitness (Crone 2001). It is problematic that little is known about survival, especially of passerines (Marshall et al. 2000), considering the need for accurate demographic modeling in avian conservation.

Accurate survivorship estimation using mark-recapture depends on: (1) the marked sample being in the search area, (2) a reobservation probability of 1.0 if an individual is alive, and (3) identifying dead individuals or lost markers (Kendall and Nichols 2004). These conditions are rarely satisfied because of emigration (e.g., Cilimburing et al. 2002), unequal reobservation probability (Carothers 1979), and the improbability of finding dead individuals or lost markers. Search efforts outside of the capture area to account for emigrants provide more accurate apparent survivorship estimates, and improved model precision (Cilimburing et al. 2002, Cox and Jones 2010). Yet, few studies attempt to reobserve marked individuals over large areas (Cilimburing et al. 2002) and/or use methods to correct for movement into unobservable locations (Kendall and Nichols 2004). Apparent survival will likely underestimate true survivorship (Anders and Marshall 2005), in the absence of species-specific dispersal information, and will fail to recognize the potential bias of studying open populations in finite areas (Cooper et al. 2008).

Red-eyed Vireos (\textit{Vireo olivaceus}) breed in deciduous and mixed deciduous woodlands (Cim-
prich et al. 2000), and conifer plantations (BJW, pers. obs.) with high canopy cover (Siepielski et al. 2001). We marked Red-eyed Vireos in a large forest (~4,600 ha) in southern Ontario with the objective of assessing interannual survivorship and site fidelity. However, we re-encountered fewer individuals (11%) than would be expected based on recapture rates for other populations of Red-eyed Vireos (e.g., 54-89%; Savidge and Davis 1974). An apparent survivorship estimate calculated using our data would likely underestimate true survivorship. The low re-encounter rate we observed may be the result of low probability of re-encountering an individual that is alive as a result of interannual dispersal. We report and discuss natal and breeding dispersal distances of Red-eyed Vireos in our study area as supplemental information to help reduce bias in future survivorship estimates caused by individuals that are undetected or unobservable (Kendall and Nicholls 2004).

METHODS

We conducted our study in the ~5,500-ha Ganaraska Forest, Ontario, Canada (44° 04' N, 78° 30' W) which is composed of mixed deciduous forest and conifer plantations. We limited our activities to an approximately rectangular (3.5 × 11 km), continuously forested area (~4,600 ha).

We banded Red-eyed Vireos from 26 June to 15 August 2007 before the typical migration period in Ontario (~22 Aug to 21 Sep; Woodrey and Chandler 1997), using unique color combinations at 35 locations between 0.07 and 11.4 km apart. Nestlings (hatching year; HY), were banded once they were at least 5 days of age but before their primaries were half grown. Adults were captured in mist nets using a lure of mixed species alarm calls (Red-eyed Vireo, Yellow-throated Vireo [Vireo flavifrons], Blue-headed Vireo [V. solitarius], Red-breasted Nuthatch [Sitta canadensis], and Black-capped Chickadee [Poecile atricapillus]) broadcast using a mp3 player and amplified portable speakers. Trap sites were haphazardly established throughout the forest, generally in areas of annual nest searching and point-count activities, and where trees or shrubs provided low cover.

We classified the age of adults as second year (SY) when flight feathers were evenly worn, primary coverts were narrow with little or no green edging and, to a lesser extent, when tail feathers were narrow and tapered. We classified the age of adults as after second year (ASY) when primary coverts were broad and truncate with distinct green edging, when tail feathers were broad and not distinctly tapered, and when secondaries had a defined contrast in wear (Mulvihill and Rimmer 1997, Pyle 1997). Individuals not distinctly SY or ASY were classified as after hatching year (AHY). We classified males and females based on the presence of a cloacal protuberance or brood patch, respectively.

We attempted to reobserve banded Red-eyed Vireos during nest searching and point counts in 2008, at many but not all banding locations. One observer (BJW) actively searched for banded individuals at the 2007 banding locations from 14 June to 8 July 2008 by broadcasting a playback of Red-eyed Vireo songs for 2 min and then mixed species alarm calls for 2 min after 1 min of silence.

We calculated dispersal distances using MapSource Version 5.2 (nearest 10 m; Garmin Ltd. 2003). We measured the distance for females from the trapping location to their 2008 nest and, for males, we measured the distance from the trapping location to their nest or to where the territorial male was first observed singing when their nest was not found. We excluded two re-encountered individuals from our results. An individual banded as a nestling was reobserved 195 m from its banding location early in the breeding season (4 Jun 2008) and was not reobserved on subsequent searches. Another individual was reobserved during playback surveys but the band combination could not be clearly read.

RESULTS

We re-encountered 12 of 109 (11%) banded Red-eyed Vireos (Table 1) 1 year after banding. Two were first re-encountered using playback of mixed species alarm calls, and 10 were first observed during nest searching. One individual known to be nesting in the area was also reobserved during playback. We re-encountered more males (n = 9) than females (n = 3), and similar proportions of HY (3 of 25 banded, 12%), SY (4 of 27, 15%), and ASY (5 of 56, 9%) individuals. Red-eyed Vireos were re-encountered between 40 and 9,870 m (Table 2) from their banding location. Two HY Red-eyed Vireos banded as nestlings and an ASY male had long
TABLE 1. Number of Red-eyed Vireos banded between 26 June and 15 August 2007 in the Ganaraska Forest, Ontario.

<table>
<thead>
<tr>
<th>Gender</th>
<th>Hatching year</th>
<th>After hatching year</th>
<th>Second year</th>
<th>After second year</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unknown</td>
<td>25</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>32</td>
</tr>
<tr>
<td>Female</td>
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<td>0</td>
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<tr>
<td>Male</td>
<td>0</td>
<td>1</td>
<td>11</td>
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<td>40</td>
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<tr>
<td>Totals</td>
<td>25</td>
<td>1</td>
<td>27</td>
<td>56</td>
<td>109</td>
</tr>
</tbody>
</table>

(>2 km) dispersal distances compared to the other nine re-encounters (<350 m).

DISCUSSION

Our re-encounter rate of adult Red-eyed Vireos was low for a forest passerine, but the re-encounter rate (12%) for hatching year birds appeared high compared to the average of other studies (3.7%, SE = 0.6, n = 51 studies; Weatherhead and Forbes 1994). It is difficult to make inferences from our small sample size, but the small samples may highlight potential bias in survival estimates as a result of interannual dispersal. Most studies of marked Red-eyed Vireos have been spatially limited (e.g., one 64-ha study plot: Savidge and Davis 1974; nine 30-ha study plots: Marshall et al. 2002). Our survey included samples from across 4,600 ha and we re-encountered three Red-eyed Vireos that dispersed farther than the longest previously reported distance (545 m; Marshall et al. 2002). Most Red-eyed Vireos we re-encountered (9 of 12, 75%) moved >100 m, suggesting dispersal from the previous year’s territory (sensu Marshall et al. 2002). Thus, apparent survivorship estimates may be biased by reduced detection probabilities because of dispersal both within the study area and potential emigration from the study area.

Methodological issues biasing detection probability could have affected our re-encounter rates. We only re-encountered a few banded individuals using playbacks in the same location in the subsequent year, despite our success using mixed species alarm calls to attract vireos during initial capture. The low re-encounter rate is due to failure to attract all banded birds to the playback, brief responses to the playback, and to the generally long dispersal distances of returning birds. For example, we were able to attract two banded males with active nests <170 m from the playback, but we did not attract a third male also with an active nest within 70 m. Another individual responded to the playback but not sufficiently long to read the color markings. We re-encountered most birds beyond the maximum distance that birds appeared to respond to the playback (>170 m) which suggests a systematic search of larger areas around all banding locations would have probably increased our re-encounter rate. There is some concern that searching large areas may be inefficient (Cox and Jones 2010) or that models accounting for dispersal may overestimate apparent survivorship (Cooper et al. 2008), but long-distance adult and natal dispersal of Red-eyed Vireos must be recognized in future investigations.

TABLE 2. Interannual dispersal distances (m) of Red-eyed Vireos in the Ganaraska Forest, Ontario. Age at banding is shown.

<table>
<thead>
<tr>
<th>Hatch year</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9,870°</td>
<td>4,090°</td>
</tr>
<tr>
<td></td>
<td>70°</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Second year</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>350°</td>
<td>250°</td>
</tr>
<tr>
<td></td>
<td>200°</td>
<td>170°</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>After second year</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2,045°</td>
</tr>
<tr>
<td></td>
<td>350°</td>
</tr>
<tr>
<td></td>
<td>40°</td>
</tr>
<tr>
<td></td>
<td>50°</td>
</tr>
<tr>
<td></td>
<td>220°</td>
</tr>
</tbody>
</table>

Mean ± SD: 4,970 ± 6,930; Median*: 4,970

1 Males observed on territory but no nest found in 2008.
2 Distance measured to nest.
3 Median for age group irrespective of gender.
AKNOWLEDGMENTS

We thank C. M. Falconer for help with banding and reobservations, and D. C. Tozer, M. R. Marshall, and an anonymous referee for insightful comments on earlier drafts of the manuscript. We also thank the Ganaraska Region Conservation Authority for access to the study area and the Oak Ridges Moraine Foundation for providing funding supporting this research.

LITERATURE CITED


Evening Nest-box Departure Times of Eastern Screech-Owls

Werner G. Deuser

ABSTRACT.—I observed 514 nest-box departures of 12 different individual Eastern Screech-Owls (Megascops asio), both males and females, at dusk in Falmouth, Massachusetts over a period of 12 years and compared their departure times to local sunset.

Mean (± SD) delay after sunset was 21 ± 12 min, identical for males and females, but longer than those reported for more southerly locations. Females departed significantly earlier on overcast evenings. Females advanced their departure times during the nestling period by as much as 2.6 min/day, on average, over a 25-day period. The observed differences in departure delays among populations in Texas, the Washington, D.C. area, and Massachusetts may be an expression of...
The first systematic observations of the relationship between sunset and evening departure of a pair of Eastern Screech-Owls (Megascops asio) were made by Allard (1937). He reported that, from 19 March to 21 May, the departures of both the male and female averaged 7.8 min after sunset on clear evenings and 7.4 min before sunset on cloudy and stormy evenings in the Washington, D.C. area. He also noted the male left earlier than the female and that, during the nestling period, both sexes left the box earlier with respect to sunset than during the pre-hatching period and suggested this was due to the food need of the hatchlings. Gehlbach (1994) reported that, during the December to February period, males in central Texas departed from their nest boxes 15.2 ± 4.1 min after sunset and that a female left 3 to 24 min after her mate. He also made light-level readings at the times of a male's departures from a roost box and a roosting tree and found the means of the readings to be independent of cloud cover. More recently, he found that stored food in the nest box had a greater effect on timing of departure than cloud cover (F. R. Gehlbach, pers. comm.). Relationships between nest departures and sunset have also been reported for other owls, e.g., Long-eared Owl (Asio otus) (Wijnands 1984), Flammulated Owl (Otus flammeolus) (Hayward 1986), Ural Owl (Strix uralensis) (Korpimäki and Huhta 1986), Short-eared Owl (Asio flammeus) (Bosakowski 1989), and Mexican Spotted Owl (Strix occidentalis lucida) (Delaney et al. 1999).

I attracted Eastern Screech-Owls (Megascops asio) to a nest box in my back yard in a heavily wooded section of Falmouth, Massachusetts (41° 32' N, 70° 36' W) starting in 1999. I recorded the consistency of the timing of their evening departures with respect to sunset and the differences, if any, between individuals, clear and overcast evenings, males and females, and between roosting and nesting individuals. I also examined differences among the departure times of birds in Texas, the Washington, D.C. area, and my Massachusetts data.

METHODS

I recorded 514 nest-box departures at dusk between 18 April 1999 and 21 May 2010. I did not want to disturb the birds and had no way of marking them individually. I used the following criteria to distinguish between males and females: (1) color morphs (all but one pair were of different colors), (2) positions during mating, which was observed six times, (3) residence outside (males) or inside (females) the box during incubation and nestling periods, and (4) pitch of their vocalizations; females have distinctly higher pitch (Miller 1934, van der Weyden 1975, Cavanagh and Ritchison 1987, Gehlbach 1994). Unpaired individuals could be distinguished by (1) color morphs (I had gray, brown [lighter and darker shades] and rufous individuals in residence, and (2) behavioral differences. In confrontations with gray squirrels (Sciurus carolinensis) at the entrance to the box, some roosting (not nesting) individuals fled the box, while others stood their ground and chased the squirrels away. These behavioral differences were matched by differences in color morphs in several cases and are a valid criterion, even for individuals of the same color. I conclude, based on these criteria, that of the 26 birds I observed separately at different times over the 12 years of the study, I had a minimum of 12 different individuals in residence and, except for 32 instances, was able to distinguish the gender of birds departing the nest box. The 32 exceptions were of individuals that roosted in the box for brief periods, did not have a mate, and did not vocalize.

RESULTS

The first resident owl in some years, usually a male, failed to attract a mate or abandoned the box. Pairs were resident in 1999, 2000, 2001, 2002, and 2010. Two nestlings fledged in 2000, and four each in 2002 and 2010. The hatchlings fell prey to a common raccoon (Procyon lotor) in 1999, and in 2001 the eggs must have been infertile, as the female prolonged incubation for 41 days.

The times of 514 nest-box departures (Fig. 1) cluster near local sunset as given in a web site of the U.S. Naval Observatory in Washington, D.C. The data cover 7.5 calendar months, a few days short of the full amplitude of the annual daylight cycle. The sunset curves for all years, including leap years, are identical. No owls were resident in the nest box between 8 June and 22 October of any year. Both adult and young owls roosted outside the box after fledging and no adults ever returned to the box until late October at the
FIG. 1. First nest-box departures of male and female Eastern Screech-Owls in 1999–2010 compared to local sunset, EST (solid curve), Falmouth, Massachusetts.

The distribution of the departure times is shown in Fig. 2. The mean (± SD) delay between sunset and departure time was 21 ± 12 min. Most departures before sunset occurred during the nestling period, i.e., late April through early June.

when with very few exceptions, only the female resided in the box (Fig. 3). There was no significant difference across all years between departure delays of males and females, relative to sunset (Table 1). The same is true for individual years outside the nestling period. For example, mean (± SD) male departure delay in 2010 was 21.72 ± 10.02 min, and mean female delay was 21.73 ± 5.72 min (Table 1). However, when both birds were in the box, mainly during the early stages of the nestling period, the male was the first to leave (by 22.9 ± 16.7 min, n = 13). Males spent the days hidden outside the box during most of the nestling period, but within sight of it. The female’s departures prior to the nestling period on clear nights in 2010 were significantly (P = 0.05) later than on cloudy nights, whereas there was no significant difference for the male (Table 1). Females had a consistent trend towards earlier and earlier departures as the nestling season progressed, averaging as much as 2.6 min/day over a 25-day period (Fig. 4, all P < 0.01).

**DISCUSSION**

There was a tight correlation (r = 0.98) between times of sunset and first departure from the nest box throughout the amplitude of the annual daylight cycle, suggesting the owls time their departures quite consistently to a certain ambient light level. Significant deviations occurred exclusively during the nestling period. The distribution of the departure times relative to sunset was near normal (Fig. 2) with the left-hand tail (early departures) representing the latter part of the nestling period, and the right-hand tail (late departures) mostly representing the early part of the nestling period, during which the female broods the nestlings. Late departures may also be due to an abundance of food in the box (F. R. Gehlbach, pers. comm.). I did not inspect the nest box while birds were in residence and judged the beginning of the nestling period by the first observation of food deliveries by both adults, and its end by the departure of the last nestling. The duration of the nestling period was 31 days in

**TABLE 1** Nest-box departure delays (minutes) of Eastern Screech-Owls relative to local sunset, 1999-2010. Falmouth, Massachusetts.

<table>
<thead>
<tr>
<th>Category</th>
<th>Mean ± SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males (all years)</td>
<td>20.56 ± 9.99</td>
<td>262</td>
</tr>
<tr>
<td>Females (all years)</td>
<td>21.65 ± 14.46</td>
<td>220</td>
</tr>
<tr>
<td>Male (2010, all nights)</td>
<td>21.72 ± 10.02</td>
<td>60</td>
</tr>
<tr>
<td>Female (2010, all nights)</td>
<td>21.73 ± 5.72</td>
<td>18</td>
</tr>
<tr>
<td>Female (2010, clear)</td>
<td>25.40 ± 3.96</td>
<td>9</td>
</tr>
<tr>
<td>Female (2010, overcast)</td>
<td>18.07 ± 4.87</td>
<td>9</td>
</tr>
<tr>
<td>Male (2010, clear)</td>
<td>25.48 ± 8.56</td>
<td>25</td>
</tr>
<tr>
<td>Male (2010, overcast)</td>
<td>17.64 ± 9.01</td>
<td>35</td>
</tr>
</tbody>
</table>

* Pre-nestling period.
FIG. 4. Progressively early departures of female Eastern Screech-Owls from nest box during three successful nesting periods, 1999-2010, Falmouth, Massachusetts.

2000, 35 days in 2002, and 31 days in 2010. The different lengths may be dependent on availability of food, which influenced growth of the owlets, and on the number of nestlings which fledge on successive days. The observed range is in agreement with those given in other reports of Eastern Screech-Owl nesting periods, e.g., 30-32 days (Sherman 1911), 31-35 days (Kelso 1950), 30-32 days (Johnsgard 1988), and 24-32 days (Gehlbach 1994). The increasingly earlier departures of the females during the nestling period has been reported earlier (Allard 1937, Gehlbach 1994) and most likely were due to the increasing food demand of the nestlings and, presumably, the increased crowding in the nest box as the owlets grow. Neither of the adults stayed in the box during the day in the last 4 to 6 days of the nestling period, except for brief periods when they fled mobbing by other birds and sought refuge in the box.

The departure delays reported here are longer than those for more southerly locations, such as Washington, D.C. (Allard 1937) or Texas (Gehlbach 1994). The Texas data are for M. a. havr Piano, whereas my study deals with M. a. naevis (Gehlbach 2003). Allard's observations were for an area close to the intergrade zone between M. a. naevis and the nominate subspecies M. a. asio (Gehlbach 2003). The observed behavioral differences among populations of the three studies may aid in distinguishing between subspecies, but differences in length of twilight at the different latitudes, orientation of nest boxes with respect to sunset azimuth, and different foliage canopy may also have a role. The lack of any significant difference between male and female departure times appears to be unique to this study.

ACKNOWLEDGMENTS

I thank F. R. Gehlbach for helpful correspondence during the early years of this work, R. R. Eakin, A. B. Hennessey, Ivan Valiela, and D. W. Holt for comments on the manuscript, and C. E. Braun for careful editing.

LITERATURE CITED


GEHLBACH, F. R. 2003. Body size variation and evolution-
Carrion-feeding by Barred Owls (Strix varia)

Joshua M. Kapfer,1,4,5 David E. Gammon,2 and John D. Groves3

ABSTRACT.—Few documented reports exist that describe carrion-feeding by owls. We produce a conclusive record of carrion-feeding by Barred Owls (Strix varia) from photographs taken with a passive-infrared wildlife camera trap baited with the whole or partial carcasses of road-killed mammals (eastern gray squirrel [Sciurus carolinensis] and white-tailed deer [Odocoileus virginianus]). We recorded multiple pictures in two documented occurrences (one in Oct 2010 and the other in Dec 2010) over multiple days of a Barred Owl visiting both fresh and mostly-decayed carcasses. Attempts to lure owls to camera traps through use of tainted chicken and turkey meat were unsuccessful, and no additional owl pictures were obtained from unbaited cameras throughout 2010. Received 21 January 2011. Accepted 19 March 2011.

Scavenging, or carrion-feeding, often has a key role in ecosystems (DeVault et al. 2003, Setiya and Fortuna 2007). Some birds, such as New World and Old World vultures, specialize on carrion-feeding (Houston 1979, Hiraldo et al. 1991). Many other predator species also scavenge to a lesser extent (DeVault et al. 2003). This interesting foraging behavior remains poorly documented for most predator species, as common research methods for diet analysis make it difficult to ascertain if prey was killed or scavenged (DeVault et al. 2003). Work has been done to assess carcass removal rates by scavengers in agricultural and natural habitats (e.g., Balcomb 1986, Linz et al. 1998, Kostecke et al. 2001, DeVault and Rhodes 2002, Prosser et al. 2008, Ponce et al. 2010), but researchers rarely track the fates of specific carcasses to know which species are responsible for scavenging (but see Kostecke et al. 2001, DeVault and Rhodes 2002).

Scavenging among owls has been documented for only a handful of species (Eckert and Karalus 1987, Voous 1988, Duncan and Duncan 1998, Díaz-Ruiz et al. 2009), and usually without much detail. The Birds of North America species accounts report carrion-feeding for only two of 19 species of North American owls (Northern Hawk Owl [Surnia ulula], Duncan and Duncan 1998; Great Horned Owl [Bubo virginianus], Houston et al. 1998), and long-term meat storage is reported for 18 of these species (Poole 2005). The risk of disease from eating rotten meat should be similar whether or not the meat was killed by the foraging owl. Given that long-term meat storage seems to be the rule among owls, why should so few reports exist for carrion-feeding in owls?

Carrion-feeding may present additional risks not associated with food-storage, such as competition with other scavengers. Owls use visual and auditory cues while hunting, which animal carcasses do not exhibit, and scavenging may be
opportunistic. Conversely, the lack of evidence for scavenging by owls might represent lack of attention by researchers. Most owls forage nocturnally within forests, making it difficult for humans to monitor their behavior in real time. Common techniques for studies of owl diets, such as analysis of owl pellets or stomach contents, do not easily lend themselves to ascertaining whether prey were killed versus scavenged (DeVault et al. 2003).

To our knowledge, no conclusive reports of carrion-feeding by Barred Owls (Strix varia) have been reported. Forbush (1925: 206) reported tangentially in a single sentence that Barred Owls eat carrion, but provided no details or supporting documentation. We document the first conclusive evidence of carrion-feeding by Barred Owls using passive-infrared sensor (PIR) camera traps.

**OBSERVATIONS**

On 23 September 2010, a PIR camera trap (Cuddeback Capture, white-flash; Non-Typical Inc., Green Bay, WI, USA) (128.6 m² cone of detection; delay time between photographs set at 30 sec) involved in a vertebrate inventory project was deployed on a parcel of county-owned property (Alamance County Recreation and Parks Department, Alamance County, North Carolina, USA). The main use of the property was outdoor recreation (primarily hiking), and had been exposed to either no, or limited, disturbance for several decades. Dominant habitat on-site was primarily upland mixed deciduous hardwood forest with sporadic isolated stands of various species of pine (Pinus spp.). The camera trap was mounted ~5 m from a public utility transmission line right-of-way that bisected the property. The camera was affixed at a height of 25 cm to the trunk of a deciduous hardwood tree along a game trail perpendicular to the right-of-way. No attempt was made to lure wildlife to the camera with animal carcasses, and no pictures of avifauna were obtained prior to 13 October 2010. Barred Owls had been heard on-site by JMK in April 2010, but had not been observed.

On 13 October 2010 at ~1630 hrs eastern standard time (EST), an intact dead-on-road white-tailed deer (Odocoileus virginianus) was collected ~14 km south of the study site. This carcass was wired to a stake in front of the camera at 0943 hrs on the same date. A Barred Owl was photographed visiting these remains once at 2301 hrs on 18 December 2010. A series of three pictures of Barred Owls visiting the remains were obtained on 30 December 2010 from 2238 to 2254 hrs. A Barred Owl also visited the carcass 37.5 hrs (~1.5 days) and 325 hrs (13.5 days) post-deployment, respectively. The rib cage and spine remained largely intact when the camera was removed from this location on 8 February 2011 at 1059 hrs.

Another attempt to lure wildlife near the camera with a road-killed squirrel carcass was made on 9 December 2010. The carcass was eventually removed to an unknown location by other scavenging wildlife, but Barred Owls were not attracted to the location. For comparison, we also deployed a variety of other scent and food lures near this camera, including tainted cooked post-collection, indicating rigor mortis had begun. The squirrel was placed in a five-gallon bucket on 14 October 2010 and transported to the study site ~16 km north of where it was obtained and was placed in front of the camera trap. The carcass was secured to a stake at ground level with wire. No attempt to mask researcher scent was made when deploying the carcass.

An adult Barred Owl of unknown sex was first attracted to the squirrel carcass on 19 October 2010 at 0439 hrs and captured by the camera trap (Fig. 1). This was ~115.5 hrs after the carcass was deployed and ~133.5 hrs (~5.5 days) after the estimated time of death for the squirrel. Over the next 107 min (0439 to 0626 hrs), six more pictures of an owl were captured by the camera. That evening over a 143-min period (1925 to 2148 hrs), seven more pictures of a Barred Owl were captured by the camera trap. The following evening (20 Oct 2010), a single Barred Owl was again photographed at 1953 hrs. This final attempt on the carcass was recorded roughly 155 hrs after the carcass had been deployed and ~173 hrs (slightly over 7 days) after the estimated death of the squirrel. All 15 pictures showed a single Barred Owl of similar size, eating or attempting to fly off with the carcass. Only a small amount of the carcass was still present when the camera was serviced on 21 October 2010 at 1024 hrs.
chicken meat and portions of an uncooked turkey carcass originally for human consumption. These did not attract Barred Owls prior to being consumed by other species of wildlife. No incidental pictures of Barred Owls were taken on eight additional camera traps (none of which was associated with carcasses) deployed at various sites within Alamance County, North Carolina throughout 2010.

DISCUSSION
Well-documented reports of owls eating carrion are uncommon, particularly for Barred Owls. We are aware of an anecdotal observation of a Barred Owl feeding on a roadside carcass in North Carolina (Halley Buckanoff, pers. comm.). Many owls are annually injured by vehicles along roadsides. For example, from 1979 until early 2011, ~2,500 owls that had been injured by vehicles were brought into rehabilitation centers in North Carolina (R. W. Chamberlain and D. E. Scott, unpubl. data). Of these, >1,400 were Barred Owls, the remainder were Great Horned Owls and Eastern Screech-Owls (Megascops asio). Specific evidence that these individuals were feeding on roadside carrion was lacking, and it was assumed the owls were injured while hunting. However, it is possible that some of these owls were attracted to or feeding on carrion when injured. The tendency for owls to feed along roadsides on road-killed animals may be an important conservation concern.

The advantages of scavenging over predatory behavior are substantial (e.g., lack of antipredatory behavior, low handling costs). Thus, it is not surprising that a wide diversity of predaceous species also engage in facultative scavenging (DeVault et al. 2003). Our report is the first to provide conclusive documentation for scavenging behavior in a well-known forest predator, the Barred Owl.

Camera traps are used by researchers for a variety of purposes, including species inventory/monitoring, population studies, spatial analyses, and studies focused on rare or elusive species (e.g., Mohd-Azlan and Sanderson 2007, Tobler et al. 2008, Rovero and Marshall 2009, Royle et al. 2009). Attempts to rigorously test or quantify the scavenging behavior of raptors (specifically owls) with camera traps are uncommon (Kostecke et al.
Our observation further demonstrates their value in studying scavenging behavior.

ACKNOWLEDGMENTS

We thank H. D. Gammon for his role in collecting carcasses. We thank the Alamance County Recreation and Parks Department (particularly B. T. Baker, J. B. Hagood, and R. M. Graves), as well as the Haw River Trail Partnership for allowing access to conduct the surveys that led to this observation. Equipment was purchased with funds allotted by Elon University. We thank the Carolina Raptor Center (Charlotte, North Carolina) and Wildlife Rehab Inc. (Greensboro, NC, USA) for providing data on owls injured along roadsides.

LITERATURE CITED

EVOLUTION AND TAXONOMY OF WHITE-CHEEKED GEESE. By Bertin W. Anderson. Avar Books, Blythe, California, USA. 2010: 495 pages and 24 color plates. ISBN: 0-9708504-4-1. $30.00 (soft cover), $40.00 (hard cover).—In 2006 and 2007, two volumes on White-cheeked (more generally 'Canada') Geese (Branta canadensis s. l.) by Harold C. Hanson described and named more than 200 subspecific taxa in six species in this complex. Both volumes were published posthumously by B. W. Anderson, who also contributed extensively to the second volume, essentially completing it for his friend and colleague Hanson. Now we have a volume that extends and justifies Hanson's work and presents Anderson's own independent studies of these geese. I earlier reviewed both of Hanson's books (Wilson Journal of Ornithology 119: 514–517, 2007; 121:658–660, 2009).

Anderson begins (page 4) by presenting a brief review of the historical classification of White-cheeked Geese (hereafter W-c G), starting with that by Conover in 1948 (Field Museum of Natural History Publication, Zoology Series, Volume 13, Part 1, Number 2)—and gets it wrong. Conover used the English name Tundra Goose for Branta i. leucopareia, not Aleutian Goose as stated by Anderson; that subspecific name was not then restricted to W-c G in the Aleutian Islands. Conover included the subspecies occidentalis in the species leucopareia, not in canadensis as stated, included four rather than three subspecies in canadensis, and did not recognize or even mention "the extinct kurilensis of the Kuril [sic] and Commander Islands" which was never named that (presumably = Branta hutchinsii asiatica Aldrich, 1946). Thus, Conover recognized eight, not nine, taxa of W-c G. This beginning does not instill a great deal of confidence in what follows.

The history continues with Delacour's 1954 Waterfowl of the World—skipping his basic 1951 taxonomic work in American Museum Novitates 1537—and covers several other compendia, mostly based on Delacour, by authors not generally considered alpha taxonomists. Absent is any mention of the 1957 Fifth Edition of the AOU Check-list, which is frequently discussed in quite negative terms in later pages. On page 7 there is a review of the present "commonly assumed" (apparently 1957) taxonomy, except that "The west coast of Canada and s Alaska is occupied by B. c. vancouverensis and B. c. occidentalis." There never was a subspecies B. c. vancouverensis until Hanson's second (2007) volume, where the name is proposed in such a way as to deliberately make it unavailable.

The introduction concludes with a chapter-by-chapter synopsis of how the author intends to support Hanson's work and (page 10), "to put forward a mechanism that would explain the evolution of the diversity of white-cheeked geese and to test this idea with reasonable samples... from across the continent." I attempt to follow his outline and examine how well he succeeds, although it would be quicker to report the next several chapters reveal the current AOU subspecific taxonomy is not correct because those subspecies are composed of smaller subpopulations that are distinguishable from one another. It seems necessary to note that the term 'AOU subspecies'—seemingly referring to the 1957 Check-list, the last to use subspecies, apparently means the allotment of subspecies to the species canadensis and hutchinsii when those taxa were split in the 2004 Supplement, where subspecies of Delacour 1954 were listed rather than those of AOU 1957 for the sake of a more complete listing of names.

Chapter 2 explores the extent of variation within populations as background for later analyses of variation among populations. Because the word 'population' has been used in many different ways. Anderson prefers to use the term 'taxon' (or 'taxa'), defined (page 15) to equate it to subspecies, or occasionally to species. Sixteen color and pattern characters, seven measurements, and three ratios are defined, that are used in comparisons throughout the book. Plumage characters are evaluated for individual birds by scores of either 1–3 or 1–8. Table 2.2 gives the proportion (%) of birds with each score for each character for either 3,408 (page 17) or 3,368 (page 20) specimens in five species designated by Hanson. Curiously, the fact that 0.000% of birds...
have a score of 4, 5, 6, or 7-8 is noted for each character scored on a 1-3 basis, so approximately half of the two-page table is composed of zeros. One line separating the groups of five species is wrongly placed, and the bottom line is omitted in the first page. The latter portends a problem with the tables throughout the book, which apparently were composed in a larger format and pasted into a book with smaller pages, where they don't always fit and often result in very small print.

An analysis of pairwise comparisons of these color characters shows they are virtually independent with few correlations between variables. Where there is some correlation in large geese, there is a similar correlation in small geese. Correlations between measurements are much greater than between color characters. There may be correlations between measurement and color characters (page 27), but the presumably definitive statement on that is an incomplete, indefinite, sentence. The point is made that both color/pattern and measurement characters should be considered when evaluating geographic variation in W-e G, and "the potential for geographic variation is large."

An analysis of age and sex variation in W-e G shows that (page 40) "colors and patterns are virtually useless in separating the age and sex classes." I do not understand the following statement: "However, as additional age or sex classes are added the range of variation is somewhat increased within a taxon." Within a taxon, males are larger than females and adults are larger than immatures, although there is much overlap.

Chapter 3 is a study of the effect of sample size on analytical techniques, specifically discriminant function analysis (DFA). This is important because many of the taxa Hanson described were represented by very few specimens. From a large sample of a single taxon, Anderson compared two random samples of five, then two samples of 10, two of 15, and on to two samples of 70. This allowed 14 pairwise comparisons. This test was repeated for various size samples of several supposed subspecies. This exercise shows (page 62) that with small samples "there is a high probability that putative taxa could be determined to differ when in fact they are made up of individuals from a single taxon." Comparisons should be based on samples of at least 15 of each taxon. A conclusion, not specifically stated, is that this casts extreme doubt on many, if not most, of the subspecies named by Hanson in 2006 and 2007, where samples were typically quite small. Further, it casts doubt on the taxonomic purity of the large subspecific samples assembled by Anderson.

The repeatability of plumage scores, by the same observer at different times and by different workers, is tested in Chapter 4. Recall there are 16 characters with scores of 1-3 or 1-8. For 180 birds having been scored <1 or >10 years previously, there were changes in the score of ~5 characters, ~30% per bird (Table 4.1). There were more changes for birds that had been scored earlier. Some characters are more susceptible to change in score than others. Some scores were higher, some lower; the net sum of the score differences was 5-6 points, but there is no indication of what proportion this is of the total score for any bird, or whether that difference would affect the subspecific identification, but some of the birds were identified to different taxa in different scoring sessions. "The chances of making the same identification for a given specimen were 80-85%" (page 83), which does not strike me as very encouraging.

The subspecies concept in birds is intimately related to breeding areas of populations; subspecies are defined by morphological characters that differ between or among populations that breed in different geographic areas. Individuals of migratory species will not always be in breeding areas; they will occur elsewhere as migrants or non-breeders. Chapter 5 is dedicated to showing that migrant and wintering geese have taxonomic value, and that they can be used to define subspecies. This is an important justification for the work of both Hanson and Anderson, who named and accepted many subspecies on the basis of only wintering or migrant, i.e., non-breeding, birds. This result is accomplished by establishing large samples of six 'core' taxa of Hanson, which are analyzed within themselves and compared to four geographically adjacent taxa, a total of 21 taxa. The samples of core taxa are composed of birds with varying degrees of certainty of relationship to breeding areas, from birds banded as goslings (and later collected as adults) to (page 88) "banded birds wintering at Cibola NWR that resembled birds banded as goslings ... or as molt migrants...." Table 5.1 shows the makeup of all samples. Of the 1,019 birds, fewer than 300, mostly of the core taxa, had fairly firm evidence of representing breeding populations. Most of the rest were either molt migrants or wintering birds. Some
wintering birds were assigned to a core sample on the basis of phenotypic similarity to banded birds. Within-taxon analysis of subsamples of the core taxa (the plumage characters mentioned earlier) showed that wintering birds were not distinguishable from the known breeding samples—an unsurprising completion of the circle. The core taxa are distinguishable from most of the four surrounding taxa. The conclusions of this section seem to provide a mixed message. On page 101, there are cautions against recognizing taxa on the basis of small samples of wintering specimens. On page 103, “Use of wintering specimens to make taxonomic decisions is as accurate as when using birds from the breeding grounds.” Nonetheless, Anderson concedes (page 105) that “Hanson has named perhaps 4% too many subspecies where samples of 20 or more are involved.” There seems to be no conceptual distinction made between assigning winter specimens to a named subspecies, and defining and naming a subspecies on the basis of wintering specimens.

A major conclusion of this analysis is that the AOU subspecies moffitti and canadensis are geographically variable and, thus, are not taxonomically valid as currently construed. Curiously, the author wonders (page 106) “where did the original taxonomists who named them go wrong?” It is true that Linnaeus had a small sample (introduced birds) when he named the species, eventually subspecies, canadensis and probably did not recognize the extent of variation, but Anderson’s statement suggests a total lack of understanding of how the entire pre-Hanson subspecific treatment of geese developed.

Table 6.1 is a comparison of Hanson’s taxa and those of the AOU—a welcome approach to a synonymy of Hanson’s many names. For each AOU subspecific name there is an alphabetical list of Hanson’s included taxa with a “potential” natal area and number of specimens. What the latter refers to is neither explained nor obvious; the number is frequently “zero”, and occasionally “?”. The AOU race occidentalis is included in fulva, although the former has priority if the two are lumped. The name taverneri is in the AOU list although the AOU did not recognize that subspecies. Included with Hanson’s subspecies are several names not used by Hanson but that are used, although never formally defined or proposed, in this volume. There is some confusion in listing some Hanson names in either parvipes or interior. There is a series of 20 Hanson names whose association with AOU names is ‘uncertain’ and for several others it is ‘?’. Again, vancouverensis is incorrectly used as an AOU name. The AOU subspecies leucopareiu is elevated to species rank (as did Hanson) but minima is either ignored or merged with hutchinsi. This is an unsatisfactory synonymy in many respects. The rest of Chapter 6 is devoted to pairwise comparisons of the amount of variation in the AOU subspecies, showing that the forms minima, fulva, and occidentalis are diagnosable from one another and the rest of the taxa but the rest are not separable from one another because of the great amount of variation in each.

Analyses of segments of AOU populations in Chapter 7 show the individual segments (actually Hanson subspecies) are distinguishable from one another even though the larger populations are not. This seems to be essentially a repeat of the analyses of Chapter 5. Chapter 8 shows that variation in the large forms of W-c G does not fit a pattern of clinal variation, contrary to statements and assumption of many past workers. In small geese, there is a trend of increasing size with increasing longitude east of Alaska (Chapter 9).

Chapters 10 presents a cluster analysis of large W-c G, which results in a dendrogram purporting to show the relationships of 71 of Hanson’s taxa plus four recognized but not formally named by Anderson, including 2,555 individuals (also said, and counted, to be 74 taxa). The data are from pairwise comparisons using discriminant function analysis from earlier in the book. The dendrogram is interpreted as consisting of nine major stems, each with one or more minor stems. Each major stem (or clade) includes 3–16 phenotypically similar taxa, which may be widely separated geographically and associated with one of seven AOU subspecific taxa or two of Hanson’s species level taxa. Chapter 11 does the same kind of analysis with 1,712 individuals in 54 taxa (55 by my count) of the small W-c G, resulting in six stems of Hanson taxa in five AOU subspecies or three of Hanson’s species. As summarized, this analysis groups taxa described by Hanson on the basis of phenotypic characters with clusters of similar taxa having wide, disjunct distributions, these similar taxa are separated by clusters of other taxa, in other clusters, in something of a patchwork pattern. Anderson assumes (page 233) this “phenotypic similarity indicates evolutionary relatedness.” Both the word and the concept “convergence” seem to be absent from the book.
Chapter 12 sets forth a scenario to explain the evolution of W-c G. This involves a wave of distribution, first from west to east, starting with the origin of the complex, perhaps before the first Pleistocene glaciations, and from south to north as glaciers retreated. Having reached the east, the population wave rebounded back westward. As the evolving populations moved they would find already occupied habitat or collide with a population moving another direction, and might not find suitable unoccupied breeding habitat for some distance, thus being separated from their closest relatives by intervening unrelated populations. These waves would have continued through the Pleistocene with new patches of habitat newly opened for colonization with the retreat of glaciers. This pattern explains why geographically adjacent populations are not phenotypically similar, and why continental variation in the W-c G is not clinal, as noted in earlier chapters. A major problem with this interesting hypothesis is that breeding areas for most of these “taxa” are unknown, according to Hanson’s original descriptions. Anderson gives latitude and longitude for each of them (Tables 10.2 and 11.2), but these can be based only on Hanson’s conjectures of breeding range of taxa that he named solely on the basis of migrant or wintering birds. Without knowledge of the actual breeding areas of all subspecies, this patchwork scheme unravels.

This analysis sets the stage for a revision of the taxonomy that Hanson had proposed. A synonymy of Hanson’s subspecies with AOU races is given again in Chapter 13; this one differs in substantial ways from that in Table 6.1 with different lists of Hanson’s taxa under each AOU subspecies. Anderson’s own recommended classification, presented in Tables 13.4 and 13.6, elevates canadensis and hutchinsii to superspecies representing large and small W-c G, respectively. Each major stem from the dendrograms of Chapters 10 and 11 is considered a species—nine in canadensis and six in hutchinsii, for a total of 15 species in the W-c G complex. He uses some of Hanson’s subspecific names for these species names, continuing to recognize others, and currently used AOU names, as subspecies. There is no characterization of these species level taxa or indication of geographic range. This cannot be considered a validly proposed classification because the author ignores all rules (e.g., priority) of the International Code of Zoological Nomenclature.

The final chapter in the book is a guide to identification by region, as not all taxa will be found throughout North America. This is accompanied by 23 color plates each showing dorsal and ventral views of specimens of 4-5 taxa. These plates give a good idea of the range of variation in color in the complex.

Finally, a word about the Literature Cited and the Index. Some entries in the Literature Cited lack dates of publication, names of all authors, or complete titles, or give erroneous pagination. While drafting this review I had occasion to try to find mention of Wilks’ Lambda in the text. It is not in the index under either word, but the name of an author caught my eye. Three page references were to citations of papers by that author, and two were to that author’s name in the Literature Cited. Not recalling that I have ever seen the Literature Cited indexed, I checked further, for other authors and for some keywords. The indexing of authors’ names is haphazard, but among other points there are five pages under “management” in the index that point to use of that word in citations in the Literature Cited, such as Journal of Wildlife Management. Under “wildlife management, managers” six indexed pages are all in the Literature Cited where a journal is cited, none to the text of the book. Software run amok.

Anderson’s primary statistical tool (page 55), used throughout the study, is discriminant function analysis. One statistic used in this analysis, to test differences between means of two identified groups, is Wilks’ lambda. This is misspelled “Wilke’s lamda” in five table headings in Chapter 2; “lambda” is correct in the text and in the tables of the next chapter, but the term is not mentioned in the rest of the book although the same analysis is used throughout. In addition to errors earlier noted in Chapters 1 and 2, I found a dozen errors there of grammar, poor or incomplete sentences, incorrect homophones, etc., not to mention questionable and confusing punctuation; there are dozens on dozens of such errors in the rest of the book. Most errors of this sort may be insignificant as far as understanding the geese is concerned, but I firmly believe that the quality of presentation of information, or production of a hook, is somehow proportional to the quality of the gathering and assessment of the information presented.

It is obvious that a great deal of effort went into this attempt to provide an understanding of and taxonomic basis for the extreme variation in the
W-c G complex. Unfortunately, the poorly defined resulting classification does not seem to offer a firm platform for further study or management of these important birds. Wildlife managers and waterfowl biologists will want to have this volume in their libraries, for the sake of completeness, along with Hanson's volumes. Those interested in evolution and biogeography will find some interesting ideas. This is not a volume I would recommend for the general reader.—RICHARD C. BANKS, Department of Vertebrate Zoology, National Museum of Natural History, P. O. Box 37012, Washington, D.C. 20013, USA; e-mail: banksr@si.edu

GREATER SAGE-GROUSE: ECOLOGY AND CONSERVATION OF A LANDSCAPE SPECIES AND ITS HABITATS. Edited by Steven T. Knick and John W. Connelly. Studies in Avian Biology Number 38. University of California Press, Berkeley, USA, xvii and 646 pages. ISBN: 978-0-520-26711-4. $95.00 (cloth).—Several of us discussed preparing a book on Sage-Grouse (Centrocercus urophasianus) and developed a prospectus a number of years ago. That prospectus was declined by a publisher. That was not the case with this present work as multiple petitions to list Sage-Grouse under the Endangered Species Act and state and federal agency support ‘forced’ the issue. Presently, both species of Sage-Grouse are listed as ‘Candidates’ for Federal listing in the United States (and one species is listed in Canada). Actual listing has not happened (too political?) and they are considered ‘warranted but precluded’ because of higher priority species.

This book consists of 24 chapters on factors that affect Greater Sage-Grouse (Centrocercus urophasianus). There is an extensive Literature Cited section at the end of the book and a useful Index prepared by Leslie A. Robb. The 38 contributors include many of the leading scientists working with Sage-Grouse over the last 25+ years with significant contributions by authors of recent (~10 years) studies. The authors represent most (7) of the states (and Canadian provinces) where the species occurs and includes state (Colorado, Idaho, Montana, Nevada, Oregon, Washington, Wyoming) and federal (USFWS, USGS, USFS, BLM) agency personnel as well as scientists from universities, NGOs, and consultants. This is definitely a peer-reviewed book (63 reviewers were involved as well as at least four editors.

Steve Knick and Jack Connelly were the major organizers and editors and made the process work.

It is difficult to know where to start in reviewing a book of 646+ pages chock full of everything possible that could affect listing of Sage-Grouse as T or E. The first sorting might be by what is most important: habitat or population dynamics. My view is that without habitat, one does not have to worry about population dynamics as there would be no populations to study. Thus, the most important knowledge logically would concern what is needed for the species to persist including in winter, spring (breeding), summer (early and late), and fall. Connelly et al. (Chapter 4) cover this material and lead the reader through the habitats used seasonally. We know from reading the chapters that about 50% of the original sagebrush (Artemisia spp.) shrubsteppe has been converted to other uses or is too degraded to support numerically strong populations of Sage-Grouse. We also know that Sage-Grouse are dependent upon sagebrush for all important life processes. Thus, one would expect that emphasis would be placed on maintaining what remains and trying to restore what has been lost or is too degraded by numerous factors (oil, gas, coal, and other mineral development; efforts to remove sagebrush by federal agencies over the last 80 years, and inappropriate livestock grazing easily come to mind). One should not be too shocked to learn from the chapters in this book that habitat loss continues due to the factors just mentioned as well as cumulative effects of roads, power lines, fences, etc. The useful habitats continue to be nibbled away by multiple uses and fragmented by every conceivable disturbance of the surface vegetation.

We would expect that scientists are working hard to restore and improve sagebrush habitats as Sage-Grouse clearly need shrubsteppe communities dominated by sagebrush and native grasses and forbs. In reviewing the chapters in this book, one learns there are only two that discuss restoration of sagebrush habitats. Chapter 23 by D. A. Pyke reviews what has been done, mostly unsuccessfully, to restore sagebrush rangelands to a semblance of their former condition. Chapter 22 by M. A. Schroeder and W. M. Vander Haegen reviews Sage-Grouse use of Conservation Reserve Program (CRP) lands in eastern Washington. The latter is promising, until one realizes the CRP lands are only temporary and can be returned to agricultural production with the next Federal
Farm Bill. Thus, there has been no real progress in restoring sagebrush rangelands despite continued loss of these lands. One can conclude that restoration is a failure and the long-term prognosis is grim as restoration takes a long time (30+ years, if it is possible). Federal agencies are very good at destroying and encouraging destruction of native sagebrush shrubsteppe but their record of restoration is abysmal. One needs to keep in mind that about 50% of all rangelands once occupied by Sage-Grouse are public lands managed by the Bureau of Land Management and U.S. Forest Service. I know of no areas where Sage-Grouse have re-established their distribution over significant areas of former habitat.

The importance of sagebrush is recognized throughout the book and several chapters cover sagebrush in depth. Chapter 10 by Miller et al. discusses the characteristics of sagebrush habitats and Chapter 11 by W. L. Baker discusses the important effects of fire on sagebrush stands. There are some differences of opinion about fire and how useful older stands of sagebrush might be. One view is that all taller, mature and overmature (or decadent, to some people) sagebrush should be managed with fire or other means to push succession to younger age classes. The other view is that fire is generally had for Sage-Grouse (there are many examples with the Snake River Plain in Idaho being really eye-opening) and wild fire should be vigorously suppressed, especially in low precipitation zones. Further, the evidence is clear that controlled burns are negative for Sage-Grouse. The knowledge that most subspecies of big sagebrush do not resprout after fire should be indicative of the effects of fire on Sage-Grouse use of burned areas (other than the edges).

There are multiple chapters on factors that affect Greater Sage-Grouse ranging from the effects of wild horses and burros, predation, parasites, diseases, potential for genetic problems, harvest, land uses, the human footprint, energy development, and environmental and anthropogenic issues. Some of these chapters were clearly encouraged by the listing agency (USFWS). Several of these are explicitly important. Chapter 9 by Walker and Naugle about West Nile virus effects on Sage-Grouse is important as this virus seems to be uniformly fatal to Sage-Grouse that are exposed to it. Fortunately, despite incidences of mortalities in multiple locations across the range of the species, the overall impact presently seems to be localized and less than expected. Energy development (Chapters 20 by Naugle et al. and 21 by Doherty et al.) is not localized, and is widespread and increasing throughout the occupied distribution of Sage-Grouse. There has been a rush to develop energy resources on Federal lands in the last 25 years (considering coal, oil, gas, and wind energy) without adequate consideration being given to reasonably predictable and actual impacts on Sage-Grouse. Formerly occupied Sage-Grouse habitats have been industrialized with easily predictable effects on all wildlife including Sage-Grouse. The two chapters on this topic are less than candid and appear to support further parceling of the habitats without fully understanding the need for winter habitat and corridors. Protection of ‘core’ areas alone is not sufficient. It is obvious that large-scale energy production in sagebrush steppe is extremely negative for Sage-Grouse.

This brings one to a logical discussion of population status and dynamics of Greater Sage-Grouse. No one agrees as to how many Sage-Grouse remain (or were present historically) even though I published the first review of what might be left in 1998. This was not popular at the time and remains very contentious. Chapter 15 by Garton et al. takes a look at and analyzes the ‘data’ based on counts of males on leks. Male Sage-Grouse conveniently display in spring at traditional sites and biologists have counted males on leks dating back to the late 1940s. Unfortunately, all used lek sites are rarely known, all known leks are not counted each spring, and it is not known what proportion of the males come to leks to display or, if present, can even be seen to be counted. The sex ratio in populations is skewed to females (they live longer than males), but there is no agreement as to the actual sex ratios. Further, useful long-term (20+ years of uninterupted counts of males attending leks) data sets are lacking in most areas where Sage-Grouse occur. Uniformity of procedures to count males, especially timing and number of counts of each lek spaced over time) was less than desired for many years. Improvements were made after 1998 when it became clear that petitions for Federal listing would materialize and there was a surge in number of leks counted and number of counts per lek. Garton et al. have tried to make sense of all of this material, even though there was a lot of ‘noise’ in the data sets. Once can argue if it would be better to use a 3- or 5-year average for models but it may not be useful to do so given the other
difficulties with the data sets. Garton et al. considered 30 populations over the range of the species and decided that 23 had sufficient data for analysis. They report that at least 13% may decline below effective population size (= 50 individuals) in the next 30 years. I suspect this is far less than reality as many populations have continued to decline since 2007 (the end of the period chosen for analysis). One can dispute an effective population size of 50 individuals and Garton et al. also considered an effective population size of 500 individuals. However, this number also seems less than compelling as relatively short-lived bird populations can collapse after 1-2 years of no or poor nest success and recruitment of young.

I would be remiss if I failed to mention Chapter 2 on the organizational structure of planning efforts for Sage-Grouse management. This chapter by S. J. Stiver reviews the structure of a ‘technical’ committee formed by the Directors of western state wildlife agencies starting in 1954. This committee went through several stages, initially to work with Federal agencies (primarily the BLM, and later included the USFS and other agencies), then to work against Federal agency plans to eliminate or greatly reduce sagebrush on public lands to the eventual point at one time of having only state biologists at meetings. Attitudes changed over time but the Western State Directors rarely got very involved and even declined at times to allow travel for participation in the technical committee; there was even a movement to combine the committee responsibilities with those of another committee (on Pronghorn management). The technical committee recognized the problems and sought to get the attention of the Directors on multiple issues dealing with protocols for collecting useful data and the importance of working with Federal agencies. A basic problem was that Directors of state wildlife agencies frequently changed and their interest was placed on higher priorities that directly affected agency income (and use of resources). Changes were slowly occurring starting in the mid-1990s and then went into overdrive after 1998 when it became apparent what was likely to happen (petitions for listing as T or E). This book is the product of those changes in the late 1990s and 2000-2008 intervals.

A glaring gap in the book is any commitment by Federal agencies, especially the Bureau of Land Management (which manages most of the public lands that still support Sage-Grouse), U.S. Forest Service, and Natural Resources Conservation Service (which spends Federal funds to improve management on private agricultural and range lands). The future of both species of Sage-Grouse is dependent on these Federal agencies working in concert with local county governments (in terms of zoning use of private lands useful for Sage-Grouse). State wildlife agencies should also have a role, but seem to be less than effective although recent action promoting conservation easements is promising. This material should have been discussed in the book.

I fully enjoyed reading all of the chapters multiple times and, despite some concern about what was included or not included, believe the book is a great step forward. There is something in it for everyone interested in the specifics about this particular species and its habitat, grouse in general, other shrubsteppe avian species, and any avian species with very specific habitat requirements. This book should be in every ornithological library and within handy reach on your bookshelf. I recommend it highly.—CLAIT E. BRAUN, Grouse Inc., 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: sg-wtp@juno.com

SYSTEMATIC NOTES ON ASIAN BIRDS 2010. Edited by David R. Wells. British Ornithologists’ Club Occasional Publications Number 5, 2010: 148 pages. $32.00 (paper).—Taxonomy, for most biologists, is an occupation akin to watching grass grow. I say this even as a systematist. I love to discover how birds are related to one another and then draw grand conclusions about their evolutionary history. But, I am not remotely interested in revising the names of taxa and all the folderol that goes with it. Once I get a ‘tree’ and understand a bit more about evolutionary dynamics, I dump the hard work of revision on others, and move to the next project. Fortunately, select groups of dedicated people derive great pleasure in sifting through articles, records, and specimens, documenting the idiosyncrasies of collectors and collections to assure proper name priority, use of Latin endings, and linear sequences of taxa. Thank goodness they are willing to do it, because bird research would be in chaos and birdwatchers clueless of advances in ornithology without their efforts.

In addition to people like me, who are simply lazy, a whole generation of evolutionary biologists
has little understanding of museum collections and taxonomy. We live in the molecular age. In the old days, only people well versed in field and collections-based ornithology attempted to define the relationships of birds. Now, everyone can estimate phylogenies, including kids who have never collected a specimen or even seen the birds they are studying. The good news is that modern molecular methods produce more accurate trees than the old authoritative methods, and rapid growth in the number of phylogeny-builders means that we are learning, at an unprecedented rate, about bird relationships. The bad news is that phylogeny production is overwhelming the few avian taxonomists with the training and desire to produce modern classifications. Moreover, few people care about this problem; the glory lies in discovery, not pedantry.

Ornithology in the Western Hemisphere regularly updates bird classification with new research findings via two formal committees of the American Ornithologists’ Union: the North American Classification Committee (e.g., Chesser et al. 2010) and the South American Classification Committee (Remsen et al. 2011). Classification revision in the Old World has not been centralized formally. Systematic studies published in various journals (e.g., Bulletin of the British Ornithologists’ Club) have been compiled periodically by a few individuals into updated classifications (e.g., Dickinson 2003). However, for Asian birds, a concerted effort to revise bird classification more regularly has been in place for 10 years. The Nationaal Natuurhistorisch Museum (Leiden Museum) and the Trust for Oriental Ornithology (TOO), starting in 2000, began publishing taxonomic reviews and revisions in Systematic Notes on Asian Birds (SNAB) under the editorship of R. W. R. J. Dekker, Edward C. Dickinson, and (more recently) David R. Wells. Five annual issues appeared in Zoologische Verhandelingen and a sixth in Zoologische Mededelingen in 2006. Thereafter funding ran out. Now, following a 4-year hiatus, SNAB is back thanks to the efforts of the TOO and British Ornithologists’ Club (BOC). It is now edited by David Wells and will be published periodically in the BOC’s Occasional Publications series.

The first product of the new collaboration is excellent. It contains outstanding reviews of some particularly difficult groups: babblers (Timaliidae) and the Old World warbler genera Seicercus and Phylloscopus; a preliminary review of grebes; and an update of a classic work on Bangka Island, Indonesia, by G. F. Mees. It is wonderful to have SNAB back in action. Indeed, I have only one complaint, which is not a criticism of SNAB per se, but rather of the genre. The new SNAB has some outstanding contributions, especially the 70-page effort on Seicercus and Phylloscopus by J. Martens, but these articles are not indexed or searchable on the web. Thus, they will not be found (at least initially) by the uninformed. Worse, the authors, who have done a tremendous amount of hard work, will not receive proper credit from citation-compiling programs, such as the Web of Science. (Universities regularly look at citation numbers on the internet to judge the productivity of their faculty.) The BOC needs to fix this problem, not only for SNAB but also for its Bulletin. That aside, ornithologists and birdwatchers interested in the latest on Asian bird classification should grab this SNAB and keep an eye out for future volumes.—FREDERICK H. SHELDON, Louisiana State University Museum of Natural Science and Department of Biological Sciences, Baton Rouge, LA 70803, USA; e-mail: fsheld@lsu.edu

LITERATURE CITED


passing the range of the species; and a larger, nearly one half of a page, distribution map, indicating breeding and non-breeding ranges if the bird is not a resident, as well as subspecies ranges. The text of each species account is divided under the following headings: genus (if the species is first in the genus), English name, scientific name, length, identification, main confusion species, vocalizations, habitat, breeding, range, status, and 2009 IUCN Red List category. The 'identification' section is brief, pointing out salient features, which is appropriate considering the many photographs. I note the white on the outer tail feathers of both Jungle (Caprimulgus indicus) and Grey (C. jotaka) nightjars is subterminal (they do not have "white tips"), a useful field mark. The 'main confusion species' sections are brief, poorly conceptualized, lacking in understanding of the difficulties of identifying these species at night, and are often not helpful. The 'vocalizations' sections are quite brief, poorly done and generally useless for identification. The 'status' sections are brief and, for the Asian species I know well, often inaccurate, especially for frogmouths and lesser known nightjars, e.g., most frogmouths are common where they are found (rather than 'possibly not common', etc.).

All eight species of Caprimulgus nightjars that occur in continental India need to be mentioned in the 'main confusion species' sections of each other as potential problems. However, this was not even minimally attempted: the Grey and Jungle nightjars are compared only to each other; none of the other seven is compared to European Nightjar (C. europaeus) and vice versa. Ditto for Syke's (C. mollhrattensis); Large-tailed (C. macrurus), and Jerdon's (C. atripennis), which are compared only to each other; the single word "none" is used in this section for both Indian (C. asiaticus) and Savanna (C. affinis). The field reality is that plumages of all eight of these nightjars are quite similar and, while there are subtle differences, the differences take time and study to master. Further, while four species (European, Syke's, Indian, and Savanna) can be differentiated visually, it is unlikely that Grey and Jungle nightjars (as well as Large and Jerdon's) can be differentiated visually from each other under most circumstances.

The well illustrated introductory section in 59 pages covers: contents, foreword, introduction, distribution of the Caprimulgiformes, plumage and structure, general biology, taxonomy of the
Caprimulgiformes, and introduction to the species accounts. There are 43 pages of useful addenda at the end of the book: glossary; further reading; acknowledgments; photographic credits (with dates and sites); Appendix 1, extinct Caprimulgiformes; Appendix 2, alternative English names; references; and index to English and scientific names (including page references for each species text and each photograph).

Utter nonsense is the statement on the front cover flap of the dust jacket that hails this book as the ‘ultimate identification guide’ to the species treated. These nocturnal birds are far more often heard than seen. This is because they tend to be highly vocal (at least during courtship and breeding seasons for migrant species and often year-round for resident species) and yet can be difficult to observe, unless you’re lucky enough to find one by day. Over 95% of the identifications of nocturnal birds that I make are based solely on vocalizations.

The birds themselves are dependent on vocalizations for identification because of the lack of visual cues at night, resulting in distinct vocalizations for each species. Thus, any guide to their identification must have a comprehensive section on vocalizations, including both detailed descriptions and sonagrams. The descriptions of frogmouth vocalizations are particularly weak. Both males and females of each species utter several types of calls, some of which are not shared, which can not be gleaned from the text.

An underlying premise of this book seems to be that once you have complete photograph coverage of all the species, little else is necessary, thus justifying the skimpy text. This is true to a certain extent since, in any given place, there are only a few of these species present. However, most of these birds are visually much alike and present identification difficulties even close up in daytime. Further, the ‘ultimate identification guide’ would also have to deal with the specimen for which there are no data. Identification could often not be made without measurements. Thus, I hope authors using this photograph format in the future will either include complete textual identification material or refrain from presenting their work as an identification guide.

Relying solely or mostly on photographs for an identification guide is not a tenable notion. The differing conditions surrounding each photo in the field, day/night, time of day, shade/open, cloudy/clear, type of film, film/digital, etc., in addition to the variation added by processing, alter the color tones of the finished photograph, and render many comparisons difficult or impossible. This is especially true of species with subtle color or pattern differences such as the nocturnal species dealt with in this book. Comparison of the different field photographs of individual species in the book shows some of the variation intrinsic to photography rather than that attributable to morphology.

A closer approach could likely be done within the present format by using the currently wasted space on each species text page, if the author is truly committed to producing the ultimate identification guide. First, the world map could be deleted entirely. Second, the distribution maps could be reduced in size by 75–85% without losing any of the detailed on them. The ‘main confusion species’ sections need to be rewritten to include vocal cues as well as a better presentation of the visual aspects. Sonagrams and complete descriptions of each vocalization could then be inserted. It would be further useful to have a series of diagnostic measurements for each species.

This volume is not a new edition of Cleere’s 1998, Nightjars: a guide to the nightjars, night-hawks, and their relatives, which covers the same species, but has a more extensive text and is illustrated by poor to average painted plates. One useful feature of the earlier work, in-flight paintings of each nightjar, is not present in the book under review, but should be.

A photographic picture book of all the species of a single (or several) families in all their diversity and glory is to be applauded and encouraged; however, the utility of an identification guide to all the world’s species of a group of birds is to be strongly questioned, with a few notable exceptions such as seabirds and shorebirds. No one is going to carry all (or even a few) of the various world family guides on a trip to a single country or continent, although they might take along some scanned or xeroxed pages. The authors of these books are rarely experienced in the field with all the species they cover as is amply illustrated by this book.

This is a fine picture book of all the species in the families included, nestled within a modern taxonomic framework. The pictures, combined with the distributions, will enable identification of some birds. However, it fails as an identification guide for the Asian species I know because of its inadequate text.—BEN F.
WHOOPING CRANE: IMAGES FROM THE WILD. By Klaus Nigge with an introduction by Krista Schlyer. Texas A&M University Press, College Station, Texas, USA. 2010: 228 pages and 156 color photographs. ISBN: 978-1-60344-209-1. $45.00 (cloth).—This attractive coffee table book is a stunning photographic tribute to the Whooping Crane (Grus americana). The images are generally presented one to a page with a few two-page spreads. While any photograph of these stately and elegant birds is likely to be of interest, this collection of images is outstanding in the breadth of behaviors and actions illustrated.

The photographs are the heart and soul of the book, but the book actually begins with an essay aptly titled "The Whooping Crane: An Introductory Primer" by Krista Schlyer. This essay is a wonderful introduction to the Whooping Crane in the real world and in mythology. The reader learns about the life history of the Whooping Crane, and the near extinction of this stately icon. The background provided in this lengthy essay increases the readers' appreciation and understanding of the photographs. It is hard to imagine a more dramatic recovery than a species which was erroneously declared extinct in the 1923 Saturday Evening Post but can now be readily observed by the general public in the winter months. As easy as it is to see Whooping Cranes in winter, it is impossible for all but a handful of people to see them in their remote native breeding areas.

The photographs are organized into three collections with separate topics in each collection. Each topic is briefly introduced in a paragraph but otherwise the photographs are presented without commentary. The first collection is from Aransas National Wildlife Refuge (NWR) in Texas, where the majority of the wild population of the Whooping Crane winters. We see Aransas NWR's tidal marshes and bays, and a few animals. The cranes are feeding, dancing, loafing, and sleeping and, in one of my favorite photos, we see a Whooping Crane grabbing the wing of a Black-bellied Whistling-Duck (Dendrocygna autumnalis) at a game feeder.

The second collection is from Wood Buffalo National Park in Alberta and Northwest Territories, Canada, the breeding area for the wild population. Klaus Nigge was granted unprecedented access to a single pair of nesting Whooping Cranes within this remote park. He was allowed to set up a blind near a crane nest where he spent 6 days ensconced 24 hrs a day in the blind so as not to disturb the cranes. We see a pair of Whooping Cranes through his lens incubating two eggs, and when one egg hatches the pair lavish attention on the chick. Another stunning series shows a Common Raven (Corvus corax) stealing the second egg as it is hatching unattended by the adults. The raven carries the egg and chick away, by carrying the egg by the chick's leg. The adults are frantic and chase the raven, but it is too late. While many Whooping Cranes only raise a single chick, the series shows the perils of the chicks' early days.

The final collection is a return to Aransas NWR the next fall. The main subjects are a pair of adult Whoopers with two cinnamon-colored offspring. We see the adults defend their winter feeding territory from other Whooping Cranes, including flocks of non-breeding birds with threat displays. There are more photographs of the family dancing, and the family at sunset in a marsh at Aransas.

There are concluding brief essays, the first on where to see Whooping Cranes. Oddly enough, this essay starts with the International Crane Foundation in Baraboo, Wisconsin and Necedah NWR in Wisconsin where Whooping Cranes from the eastern migratory introduced population can be seen in spring and summer. The last site mentioned is Aransas NWR, where the wild population winters and the winter images in this book were taken. The popular boat trips from the Rockport area in search of Whooping Cranes are mentioned, but I think they should be the first opportunity discussed and not the last. The final essay discusses the great efforts used to photograph Whooping Cranes at Wood Buffalo National Park. We see the blind, the photographer at work, and the blind in situ. In my imagination I can hear the hum of biting insects over the marsh.

This is a wonderful book with factual information, excellent photography, and a chance to peek into the private lives of Whooping Cranes. I thoroughly enjoyed the book, and I would recommend it to all who enjoy birds or are
interested in conservation. The success story of the Whooping Crane from 21 individual birds in 1941 to multiple wild and managed flocks numbering in the hundreds provides a ray of hope for other rare species.—MARY GUSTAFSON, Rio Grande Joint Venture, American Bird Conservancy, Mission, TX 78572, USA; e-mail: mgustafson@abcbirds.org

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COVER: Wilson’s Plover (Charadrius wilsonia). Illustration by Don Radovich.

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ABSTRACT.—A review of all available specimens and the discovery of many unpublished life history notes allows a much more complete picture of the morphology and behavior of the extinct Wake Island Rail (Gallirallus wakensis). The breeding season of the species may have been environmentally influenced but, under favorable conditions, there may have been two broods per year. Small groups of birds engaged in cooperative nesting and prolonged parental care and feeding of the young, probably in part to defend the eggs and young from hermit crabs (Coenobita) and rats (Rattus). The smallest species of its genus, the Wake Island Rail was able to co-exist with Pacific rats (Rattus exulans). Extinction of the rail occurred between 1942 and 1945 as a result of direct predation by thousands of starving Japanese troops and habitat destruction resulting from military alterations and aerial bombardment. Received 8 February 2011. Accepted 4 June 2011.

Wake Island or Atoll is one of the smallest, harshest, and most isolated motes of land known to have harbored an endemic species of land bird, the Wake Island Rail (Gallirallus wakensis), the smallest historically known species of its genus. These ‘serious business-like little birds,’ as they were characterized, had survived the adversities of their sun-bleached, storm-battered, and often drought-plagued corner of the planet for thousands of years, until coming to the attention of the scientific community at the turn of the 20th century. Then, before the century was half over, the species would be extinct. Wake Island was the scene of the first battle in the all-out war arising from the attempted Japanese conquest of the islands of the Pacific. For nearly 4 years, Wake was the scene of unrelenting human violence and suffering unparalleled in the history of World War II for an area so small and remote. At the end of that conflict the little rail was no more. Little has been known or written about Gallirallus wakensis and no opportunities will ever exist for further observations. The present study came about through discovery of written and photographic materials concerning the Wake Island Rail in archival sources (e.g., Fig. 1), or obscure publications that had not been consulted or incorporated into the scant accounts of the species that have appeared to date. These provide information on the species that is new and original and the statement that ‘most aspects of the life history of the Wake Island Rail ... will never be known’ (Lowe 2003:33) is no longer true. We also attempted to trace and examine all known
specimens of *Gallirallus wakensis* in museums to record as much as possible about its appearance, size, molt, etc. Detailed specimen data can often reveal a great amount about life history as well as morphology (e.g., Olson 1999a). Our objective was to bring together all existing information we could find as a final requiem for the species on the 70th anniversary of the onset of its extinction, December 1941.

**METHODS**

*Museum Specimens.*—We attempted to trace all existing specimens of *G. wakensis* in museum collections (Table 1). The first specimens were obtained by Japanese collectors for Alan Owston (1853–1915), a natural history dealer who operated out of Yokohama, Japan (Anonymous 1916). These were sold to Rothschild (1903:78), who mentioned that “a Japanese vessel obtained ten specimens in 1892,” but evidently not all 10 were made available to him at that time. Hartert (1927:22) attributed the specimens to Alan Owston’s collectors and mentioned a “type” but, because the Rothschild collection had no registry numbers, that specimen cannot be identified from his publication. He also mentioned

---

**TABLE 1.** Known specimens of Wake Island Rail (*Gallirallus wakensis*) in museum collections.

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<th>Collector</th>
<th>Dates</th>
<th>Preparation type, number, repository</th>
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<tr>
<td>Owston’s collectors</td>
<td>1892</td>
<td>Skins: 10 AMNH, 1 BMNH</td>
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<tr>
<td>Wetmore Tanager Expedition</td>
<td>28 Jul-3 Aug 1923</td>
<td>Skins: 40 (1 MCZ; 1 ROM); skeletons 3 complete, 27 trunks (1 trunk AMNH); fluid 3 complete, 6 trunks. All USNM except as noted.</td>
</tr>
<tr>
<td>Kenler</td>
<td>Nov 1935</td>
<td>Skin: 1 BBM</td>
</tr>
<tr>
<td>Spencer and Garlough</td>
<td>4–12 Jun 1937</td>
<td>Skins: 6 USNM</td>
</tr>
<tr>
<td>Brock</td>
<td>22 Aug 1938</td>
<td>Skin: 1 ANSP</td>
</tr>
<tr>
<td>Lyons</td>
<td>21 Jul, 25 Oct 1939</td>
<td>Skins: 3 (2 downy), fluid 2 (downy) MVZ</td>
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"further skins received, all from 1892" and it is no longer clear which specimens constituted the original series upon which Rothschild based the name. Ten of the original specimens went to the American Museum of Natural History (AMNH) with the sale of Rothschild's collection. Greenway (1973:307) identified the lectotype of Hypotaenidia wakensis as AMNH 545265, presumably on the basis of a Hartert label annotation. These specimens were made up with the legs far up the body and the bill pointing up, except for one that was obviously remade as a traditionally positioned and proportioned study skin. One specimen with the original preparation was received at the Natural History Museum, London, from Rothschild (BMNH 1908.12.21.7: Knox and Walters 1994).

The largest series of G. wakensis was collected on the Tanager Expedition in late July and early August 1923 (Olson 1996). Wetmore obtained 46 individuals that were prepared as 40 skins, 3 complete and 27 trunk skeletons, and 3 complete and 6 trunks preserved in alcohol and placed in the National Museum of Natural History, Smithsonian Institution (USNM). One skin from this series (Wetmore 7756, USNM 301075) was exchanged to J. H. Fleming and is now in the Royal Ontario Museum (ROM 37304) and a second (Wetmore 7834, USNM 301098) was exchanged to Harvard University (MCZ 157073). A single trunk skeleton (Wetmore 1803, USNM 499370) was exchanged to AMNH (10503). Unfortunately, Wetmore's cataloging system does not allow a trunk specimen to be associated with a given skin. Of the six trunks preserved in alcohol, we opened one (USNM 289336) to examine the condition of the gonads.

Eleven additional specimens were obtained incidentally during 1935–1939 when the island was in use mainly as a stopover for commercial airline flights prior to military buildup. The first was a single skin taken in November 1935 (Bernice P. Bishop Museum, BBM 6120) by Myron L. Kenler, a physician assigned to Wake by Pan American Airlines (Pan Am), where he was in residence from 9 May to 4 December 1935, during which time he also collected biological specimens for the Bishop Museum (Krupnick 1997). Kenler's is the only adult specimen of which we are aware that is in completely fresh, unworn plumage (Frontispiece).

H. J. Spencer and F. E. Garlough, while controlling rats in 1937, obtained a small series of seabirds and six specimens of the rail, including one juvenile, that were incorporated into the collections of the Biological Survey housed at USNM. The following year, one specimen, skinned out of alcohol, was collected by Pan Am pilot Horace Brock, who was a personal friend of R. Meyer de Schauensee, curator at the Academy of Natural Sciences of Philadelphia (ANSP), where the specimen is housed (ANSP 131672). Five specimens at the Museum of Vertebrate Zoology (MVZ) collected by Torrey Lyons consist of four downy young (2 skins, 2 in fluid) taken on 21 July 1939, and an adult skin from 25 October 1939, the last specimen of the species ever to make it into a museum. Wing measurements were made with a stopped ruler to the nearest 1.0 mm. Other measurements were made with digital calipers and rounded to the nearest 0.1 mm.

**Archival Sources.**—Official interbureau reports on the rat abatement programs on Wake Atoll are on file in the U.S. National Archives, Record Group 22, and are cited as Spencer (1936) and Hansen (1937). In August 1959, the Washington office of the U.S. Fish and Wildlife Service (USFWS) wrote to H. J. Spencer (Smithsonian Institution Archives, John W. Aldrich Papers, Accession 11-162), who was then in a branch in Gainesville, Florida, noting that his reports on rat control on Wake in the 1930s did not contain information on the birds of the island and could he supply same if possible. Spencer responded almost immediately in a report on the birds of Wake Island dated 20 August 1959, most of which had been written in 1937. We have not traced the entire report but a copy of Spencer's cover letter and the page of notes concerning the Wake Island Rail were included in Wetmore's file on the rail. We cite this material as Spencer (1959).

Alexander Wetmore’s journal of the Tanager Expedition was published in its entirety (Olson 1996) and we have cited his observations as Wetmore (in Olson 1996). A folder from Wetmore's files in the Division of Birds labeled ‘Wake Island (Rail)’ contains a variety of materials including correspondence, clippings, specimen data, and three apparently unpublished manuscripts by Wetmore concerning Wake Island and the Wake Island Rail (Smithsonian Institution Archives, Wetmore Papers, Accession 11-163). The most important of these is a carbon copy of a five-page manuscript entitled ‘Wake Island Rail Rallus wakensis (Rothschild)’ attached to a copy.
of a letter of conveyance to S. Dillon Ripley dated 28 July 1970. This was intended for Ripley’s use in compiling his work on the rails of the world (Ripley 1977). There is no evidence of any information having been derived from it in Ripley’s book, however, in which the only information from Wetmore was taken directly from his field journal. Wetmore’s manuscript contains a few observations that were not included in the published notes and we have cited it in the text as Wetmore (1970).

The most important untapped sources of information on the Wake Island Rail are the unpublished documents of Torrey Lyons. Lyons was hired as a gardener by Pan Am to grow vegetables, mostly hydroponically, for use by the airline’s hotel on Wake. He was a graduate of the Department of Botany, University of California, Berkeley, and was trained in ornithology at the Museum of Vertebrate Zoology (Rauzon et al. 2008b). He kept notes on the birds of Wake Island from 1939 to 1941, including many valuable and singular observations of the rail, of which he took unique photographs. His original journal is in the collection of field journals at MVZ. We cite his journal in the text as Lyons (with the appropriate year, day, and month), and in the Literature Cited as Lyons (1939–1941). His notes contain numerous abbreviations and idiosyncrasies of spelling and punctuation that we have at times altered for clarity. Observations attributed to Lyons not in quotation marks are as close to direct quotes as it was possible for us to make them without the use of a forest of sic’s and brackets. We also obtained previously unknown rail photographs in January 2005 from Lyons’ daughter, Tada Lyons Darsie, of Santa Rosa, California.

**PHYSIOGRAPHY AND HISTORY OF WAKE ISLAND**

Wake Atoll (19° 18′ 55″ N, 166° 38′ 21″ E) is a northern outlier of the Marshall Islands, despite its extreme isolation, 603 km from the nearest landfall at Taongi Atoll (Fig. 2). Also known as
Wake Island, the atoll is composed of three islands. The largest is the V-shaped main island of Wake (553.2 ha), the northern arm of which continues as Peale Island (103.9 ha, separated by a channel 140 m in width), and the southern arm as Wilkes Island (79.9 ha, channel 100-140 m in width depending on angle). These two islands (Fig. 2, inset) were named for the naturalist and for the commander of the U.S. Exploring Expedition by Alexander Wetmore on the 1923 Tanager Expedition (Olson 1996). The total land area of Wake Atoll is 7.4 km² (Bryan 1959). The “highest elevation is barely 21 feet (6.4 m) above sea level” (Cohen 1983:1). The windward side of the island is north, but the southern half is periodically inundated by typhoons.

The climate, soils, and vegetation of Wake were described by Fosberg (1959). The island is rather dry (~1,000 mm rain per annum) but subject to extreme droughts. The soil is mainly coraline rubble with some organic humus and the natural vegetation was low, scrubby forest dominated by Heliotropium foertherianum (formerly Turnera argentea). Bryan (1926: 4-5) considered both the fauna (especially insects) and flora of Wake Island to be “markedly different” from that of the Northwestern Hawaiian Islands and Johnston Island, and closely similar to that of coral atolls across the South Pacific.

The presence of the Pacific (or Polynesian) rat (Rattus exulans) on Wake indicates the island was almost certainly visited by far-ranging Polynesian voyagers; probably well before the 16th century. Ferdon (1987:218) argued cogently that Pacific rats were deliberately and knowingly taken by Polynesians on long sea voyages “as a marginal source of food that could fend for itself.”

It is thought the island encountered and named San Francisco in October 1568 by the Spanish explorer Álvaro de Mendaña de Neyra (or Neira) may have been the same as Wake. Beaglehole (1947:64) reported that Mendaña “sighted a small island destitute of water and bare of every living thing except sea-birds and a few stunted shrubs...and passed on in bitter disappointment.” Yet Werstein (1964:12) quoted Mendaña to the effect that “the land swarms with a strange type of rat that runs about on its hind legs.... and there are many birds of all sorts”—a passage that has been repeated by subsequent authors citing Werstein, whose quote has an aura of credibility because on Wake Island there were both Pacific rats and a flightless rail that was more or less the size and coloration of a rat and that “runs about on its hind legs.” But we found no original source for any attribution of rats to Wake by Mendaña, including in the contemporary journals of the voyage (Anheuser and Thomson 1901:lii, 69, 186, 209, 441-442). Perhaps Werstein took the rat quote from some source pertaining to another island or simply invented it.

Official discovery of the island has been credited to Captain William Wake in the British schooner Prince William Henry in 1796. Only occasional vessels sighted or visited the island from then until the beginning of the 20th century, including at least one major shipwreck in 1866 (Bryan 1942, 1959; Spennemann 2005). The only visit of a scientific nature prior to 1923 was of the U.S. Exploring Expedition in December 1841, whose naturalists reported the presence of seabirds and noted that rats were “common” but who not only overlooked the rail (Peale 1848, Poesch 1961:199) but also failed to mention the land hermit crabs (Coenobita perlata) that Edmondson (1925) described as very abundant. Wake Island was formally annexed by the United States on 17 January 1899 by a naval vessel sent from Honolulu expressly for the purpose (Bryan 1959).

A Japanese vessel visited Wake in 1892 as known only from specimens of the flightless rail that were obtained for Alan Owston who sold them to Rothschild, who named the species Hypotaenidia wakensis (Rothschild 1903). The purpose of that visit may have been to obtain feathers of seabirds for millinery purposes, possibly leading to the first voluntary human settlers of Wake Island who were among the Japanese feather poachers who ranged over the North Pacific in the early decades of the 20th century slaughtering seabirds. Two camps of feather poachers on Wake Island, apparently abandoned in 1908, were discovered and documented by members of the Tanager Expedition, who made an extensive biological survey of the island from 27 July to 5 August 1923 (Bryan 1959, Olson 1996). Alexander Wetmore, as the ornithologist on the Expedition, was the first to make any observations of the Wake Island Rail in life. He and the expedition planners, including Wetmore’s chief, E. W. Nelson of the U.S. Biological Survey, had evidently overlooked Rothschild’s (1903) brief description of Hypotaenidia wakensis and were not aware that a flightless rail should be expected on Wake Island.
Japan led to increased military activity and fortification of the island in 1940 and 1941 (Heinl 1947). It was during that period from 1935 to 1941 when numerous Pan Am employees, tourists, and military personnel encountered the Wake Island Rail and commented on it or took photographs that we assembled from widely scattered accounts and archival sources. Rat control specialists from the U.S. Biological Survey headed by H. J. Spencer, in conjunction with staff of the Hawaii Agricultural Experiment Station, worked out an agreement "in order to cooperate with the PAA [Pan Am] in ridding the islands of rats in an effort to preserve bird life there" (Hansen 1937:3). That may have been a pretext. Getting rid of rats may have been more of a cosmetic attempt to keep them from being encountered by airline passengers staying at the hotel, as rats at that time had not been demonstrated to be a threat to birds. The rat control biologists were on Wake Island during 31 July–9 August 1936, 4–23 September 1936, and 30 May–13 June 1937 (Spencer 1959).

Heinl (1947), Cressman (1992), and Kinney and McCaffrey (1995) provide a map showing runways, personnel quarters, and gun installations as they existed in December 1941. The Japanese military perceived Wake Island to be of far greater strategic importance than it turned out to be and launched an air attack on 8 December 1941 to coincide with the surprise attack on Pearl Harbor, on the other side of the International Date Line, where the date was still 7 December. The scant American forces, in one of the most valorous actions of the entire war, held off the Japanese fleet until 23 December when they were overwhelmed by massively superior numbers (Heinl 1947, Cressman 1992). The Japanese military occupied Wake Island, almost continuously under siege, until they surrendered on 7 September 1945. The island has since been a U.S. possession.

SYSTEMATICS AND EVOLUTION OF THE WAKE ISLAND RAIL

The Wake Island Rail, in plumage and proportions, is clearly a representative of the rails formerly grouped in the genus Hypotaenidia, which is widespread in Oceania and Australasia. The name refers to the breast hand found in most species, including most individuals of the Wake Island bird. Hypotaenidia was long subsumed in the nearly cosmopolitan genus Rallus, until its distinctiveness in plumage, particularly the strongly barred primaries (Frontispiece) and osteology (Olson 1973, Steadman 1987), were deemed sufficient to separate them. The flightless Weka (Gallirallus australis) of New Zealand clearly belonged with this group and the species were included under the older name Gallirallus (Olson 1973). Mayr (1949:4) considered Rallus wakensis to be among several "strikingly different" geographical representatives of the Buff-handed Rail (Rallus [Gallirallus] philippensis). Fuller (2001:127) stated that "Rallus wakensis seems to have only barely passed the point at which separate status as a species is appropriate." However, Kirchman (2009), in a phylogeny based on mitochondrial DNA, found that Gallirallus wakensis, G. owstoni (Guam), and G. ripleyi (extinct Tonga), among others, were basal to G. philippensis.

Sea Level and Evolution of Gallirallus wakensis.—Wake Atoll, with its greatest elevation at only 6.4 m, has little protection from the ravages of intense storms or tsunamis. Kaucher (1947:95), who saw the rail in August 1937, mentions that a member of her party thought all of Wake Island had once been awash, although another companion questioned that idea because of the presence of flightless rails. That the rail was absent from Wilkes Island in 1923 is a reasonably clear indication the island had been inundated and the rails wiped out sufficiently recently that they had been unable to recolonize. This evidently did not occur to Grant (1924:48) who considered that the rails were "apparently excluded from [Wilkes] by a channel six inches deep studded with stepping..."
flies at low tide" and considered that because the channel separating Wake and Peale islands was much deeper, the populations of those islands must "therefore represent independent colonies."

Wake Island would have been completely inundated during the last interglacial maximum rise in sea level during Marine Isotope Stage (MIS) 5e (Kirchman 2009), which was at least 5–6 m higher than present, and did not subside to, and remain at or below, present levels until 119,000 years ago (Hearty et al. 2007). Other taxa of flightless rails on low islands have been postulated as being no older than the last interglacial period, including the extinct Portomelops philippensis. Slikas et al. (2002) and all of the endemic vertebrates of Aldabra Island in the Indian Ocean (Taylor et al. 1979, Olson et al. 2006), including the flightless rail Dryolimnas cuvieri aldabranius. Evidence now suggests that sea levels at the end of the last interglacial (MIS 5a) rose considerably higher than previously thought (Vacher and Hearty 1989), and the latest evidence indicates 1 m above present levels at 81,000 years ago (Dorale et al. 2010). That would probably have been sufficient to inundate Wake Island during major storms. Thus, the period available for the colonization and evolution of G. wakensis may have been <80,000 years. That is not unreasonable considering that the large, endemic flightless rail Rallus recessus of Bermuda is known with certainty to have evolved well after that time, during the last glacial episode (Olson and Wingate 2001, Hearty et al. 2004, Olson and Hearty 2010). Kirchman's (2009) conclusions would therefore require the volatile ancestor of G. wakensis to become extinct in the last 80,000 years, which requires explanation.

MORPHOLOGY

Adult Plumage.—Rothschild's (1903:78) original description was: "Upper surface dark ashy brown, fading to an earthy brown: ear-coverts and lores dark brown, a pale grey superciliary line; chin and upper throat whitish, neck grey, rest of underside ashy brown, on the breast with one, on the abdomen and flanks with two or three narrow white bars; tail uniform brown: quills and under wing-coverts brown, barred with white...Wings and tail very soft, so as to suggest little power of flight." Hartert (1927:22) augmented this: "There are a number of narrow white bars, both on the sides of and across the jugulum, and the sides of breast and abdomen, also on the under tail coverts. There is a pale rufous band across the chest, indistinct in some specimens. Chin and upper throat white, middle of abdomen whitish." The undertail coverts are nearly always lacking or very worn in the Tanager series. However, the undertail coverts are distinctly barred with white as noted by Hartert (1927) in a specimen in fresh plumage (BBM 6120).

The single specimen taken in November (BBM 6120, Frontispiece) and a bird taken on 12 June are in fresh plumage except for the worn secondaries and tertials of the latter, in which the primaries have been molted. The entire dorsum is of a noticeably darker and clearer gray, approaching blackish, than in the Tanager series, which had evidently undergone weeks more of fading and abrasion so that they are browner and more scaly in appearance above (Frontispiece).

Wetmore (in Olson 1996:105) considered that "a light brown band faintly indicated across the breast" was "found in female only." In fact, a trace of a breast band is found in almost all specimens, although in some males this may be only a faintly hinted tawny wash. The breast band of females varies from indistinct to a strong ochraceous color and, in the most extreme individuals, is a clear, light chestnut (Frontispiece).

There is a considerable amount of leucism in the USNM series showing as a white spot on the upper breast between the whitish throat and the breast band (8 males, 1 female). This was but a single feather in an additional male and two females, and in one male there was a single white feather in the upper mantle. The barring of the remiges is not just white as indicated by Rothschild (1903) but is white on the outer primaries and light chestnut on the remaining remiges (Frontispiece), similar to the condition in G. philippensis.

Adult Gallirallus wakensis have been depicted in an excellent ink drawing by D. Reid-Henry (Fig. 3) in Greenway (1958), a rather fanciful, even lurid, painting in Fuller (1987:75, 2001:128–129), and color illustrations in Ripley (1977: plate 11), Taylor (1996, 1998), and Lively (2003:13). The last was based on the unsexed BMNH specimen, probably a female, which was likely the basis for all of the preceding illustrations except that in Ripley (1977), which was based on USNM 301104, a male with no breast band (USNM registrar's loan records).
FIG. 3. Pen-and-ink drawing of the Wake Island Rail (Gallirallus wakensis) from the original by D. M. Henry in the Smithsonian Institution Archives (RU 7402), originally published in Greenway (1958; figure 24).

Adult Soft Part Colors.—The bill and feet are brown (in skin) (Rothschild 1903:78). “Legs and feet brownish gray” (Spencer 1959). The eye is red, the bill is brownish gray with a pink cast, the legs brownish gray (Lyons 1939, 26 Oct). Bayler (1943:21) also described the Wake Island Rail as being “red-eyed.”

Juvenile Plumage.—Young two-thirds grown were described as “dusty black in color” (Lyons 1939, 26 Jun). The only existing specimen in juvenile plumage (USNM 7 Jun 1937, Frontispiece) appears small in body but has nearly adult measurements of bill and feet. There is no down remaining. The remiges are in sheath and are less than half grown but show the distinct chestnut barring of the adult. The dorsum is a uniform dark fuscous. The lower parts are a somewhat lighter dark gray, paler and whitish on the midline of the belly. The sides of the head and neck, except for a faint supercilium, are uniformly dark, so the brownish ocular stripe of the adult is not evident. The bill, tarsi, and toes are black, in contrast with the paler, more brownish coloration of adults (dried skin colors).

Downy Young.—All black down (not pure black but no color shade is perceptible) (Fig. 4), thin, skin black with pinkish cast. Beak and feet black, eye brown (Lyons 1939, 26 Oct). Newly hatched birds in jet black down built like a baby chick [Gallus gallus] only legs relatively shorter and wider apart (Lyons 1939, 23 Oct).

Plumage Comparisons with Congeners.—The overall plumage pattern of Gallirallus wakensis is actually quite similar to the superficially more ornate Buff-banded Rail, the most conspicuous difference being the absence of white spotting throughout the dorsum of the former. The dorsal feathers of G. philippensis are blackish with olivaceous edges. This is muted in G. wakensis to a dark hair brown with lighter, grayish margins. The ocular stripe, nape and crown of G. philippensis are chestnut, the crown suffused with black, whereas in G. wakensis these areas are a dark brown nearly concolorous with the dorsum. The underparts in the two species are similarly barred and banded, the main difference being that in G. wakensis the background barring is dark gray rather than blackish. The Guam Rail is identical in plumage pattern to G. wakensis but with darker tones. The pectoral band may be missing altogether at times in G. owstoni and the light barring of the remiges is entirely white, without chestnut. Direct evolution of plumage of G. wakensis from G. philippensis would appear to involve only loss of the white dorsal spotting and diminution in color intensity in the rest of the plumage.

Size, Morphology, and Flightlessness.—Livezey (2003), in an exhaustive quantitative analysis of the morphological manifestations of flightlessness in the Railidae, concluded that Gallirallus wakensis was small relative to its congeners (Livezey 2003), a fact that had been readily observable since the species’ discovery. Livezey’s repeated attention to ‘dwarfism’ or ‘nanism’ in the Wake Island Rail may be overemphasized, as the head size, as represented by skull and mandible lengths, is not much less than in G. philippensis.
and there is even slight overlap (Tables 2, 3). Kirchman and Steadman (2006, 2007) compared *G. wakensis* with the numerous prehistorically extinct species of *Gallirallus* described from Oceania with the only one that was as small in some dimensions being *G. ripleyi* (Steadman 1987) from Mangaia, Cook Islands. The small land area and harsh environment of Wake Atoll, where food supplies are probably diminished in times of drought, extensive overwash, or higher rat populations would have provided strong selection factors for reduced body size, whereas the head would need to be sufficiently large to obtain and process food, and to function efficiently in interspecific aggressive interactions.

*Gallirallus wakensis* and *G. owstoni* are among the few flightless rails to have lost the 10th (outermost) primary (Livezey 2003:112). The expected changes in the remiges, body plumage, and rectrices that are usually correlated with flightlessness were otherwise relatively minor (Livezey 2003: tables 27-29). The wing claw (unguis alularis) was noted to be disproportionately large in flightless rails and most notably so in smaller species (Livezey 2003:141), which accords with Wetmore’s observations that in *G. wakensis* “the wing claw in this species is very large and strong” (Olson 1996:184), and Lyons (1939, 26 Oct) that in the downy young there is a “prominent claw on front of wing.”

We know the Wake Island Rail was functionally completely flightless from behavioral observations, yet the skeletal adaptations associated with this condition are invariably moderate (Livezey 2003: tables 58–64). Thus, whereas functional flightlessness is absolute, there may be degrees of flightlessness in morphology. The extent of modification in *G. wakensis* is relatively slight, which accords with its assumed relatively recent evolution. The most obvious manifestation in the skeleton is the reduction in size of the wing and particularly in the depth of the carina of the sternum (Fig. 5), which as Wetmore noted “is very low and the breast muscles slight” (Olson
TABLE 2. Comparative skeletal measurements of three species of Gallirallus. Those for the three existing complete skeletons of G. wakensis are given individually, the first 2 being males and the last a female. In the other columns the range is given followed by the mean in parentheses. The series of G. philippensis consisted of 1 male, 2 females, and 2 unsexed specimens from Australia, New Caledonia, Halmahera, Philippines, and Palau (n = 5 unless otherwise indicated). The series of G. owstoni consisted of six males and two females, all wild-taken (n = 8 unless otherwise indicated). Measurements in boldface are greatly augmented (Table 4).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>G. wakensis</th>
<th>G. philippensis</th>
<th>G. owstoni</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull total length</td>
<td>53.9, 53.7, 48.4</td>
<td>55.6–65.1 (61.3)*</td>
<td>65.1–72.5 (68.9)**</td>
</tr>
<tr>
<td>Cranial length</td>
<td>26.3, 26.5, 24.9</td>
<td>29.8–32.7 (31.2)*</td>
<td>31.4–34.2 (32.8)**</td>
</tr>
<tr>
<td>Cranial width</td>
<td>17.6, 17.8, 17.0</td>
<td>19.1–20.5 (19.7)*</td>
<td>19.1–20.4 (19.8)**</td>
</tr>
<tr>
<td>Mandible length</td>
<td>43.5, 43.6, 37.8</td>
<td>42.4–52.0 (48.3)*</td>
<td>52.8–60.4 (55.9)</td>
</tr>
<tr>
<td>Coracoid length</td>
<td>17.3, 17.4, 16.2</td>
<td>23.3–25.8 (24.4)</td>
<td>21.7–22.5 (22.1)</td>
</tr>
<tr>
<td>Sternum length</td>
<td>26.4, 27.2, 23.0</td>
<td>38.5–42.1 (40.3)*</td>
<td>31.1–37.2 (34.9)</td>
</tr>
<tr>
<td>Sternum depth</td>
<td>7.2, 7.7, 6.5</td>
<td>14.7–16.6 (15.3)*</td>
<td>10.0–11.4 (10.5)</td>
</tr>
<tr>
<td>Pelvis length</td>
<td>31.5, 31.9, 25.8</td>
<td>37.1–41.0 (38.7)*</td>
<td>36.2–41.3 (39.2)**</td>
</tr>
<tr>
<td>Pelvis width</td>
<td>17.2, 17.4, 16.5</td>
<td>18.3–20.4 (19.0)*</td>
<td>19.5–22.0 (20.9)</td>
</tr>
<tr>
<td>Humerus length</td>
<td>33.3, 33.7, 38.0</td>
<td>45.4–49.5 (47.3)</td>
<td>41.4–44.8 (42.6)</td>
</tr>
<tr>
<td>Ulna length</td>
<td>27.5, 28.5, 25.1</td>
<td>38.5–43.3 (40.6)</td>
<td>33.8–36.1 (35.0)</td>
</tr>
<tr>
<td>Carpometacarpus length</td>
<td>18.6, 19.2, 16.4</td>
<td>25.3–29.6 (26.7)</td>
<td>21.4–23.6 (22.6)</td>
</tr>
<tr>
<td>Femur length</td>
<td>37.8, 38.7, 36.7</td>
<td>46.2–48.7 (47.6)*</td>
<td>50.4–54.1 (52.1)</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>56.9, 56.3, 53.7</td>
<td>63.4–69.5 (66.2)</td>
<td>69.2–77.0 (72.4)</td>
</tr>
<tr>
<td>Tarsometatarsus length</td>
<td>35.8, 36.7, 33.2</td>
<td>40.3–45.3 (43.0)*</td>
<td>46.7–50.6 (48.9)</td>
</tr>
</tbody>
</table>

* From naso-frantal hinge.  
† Through post-orbital processes.  
‡ Including retroarticular processes.  
§ Greatest length measured diagonally from head to external sternal angle.  
¶ Along midline but not including manubrial spine when present to posterior extent of ossification.  
‖ Through the manubrium to the tip of the culmen.  
* Midline of ventral surface of synsacrum.  
** Through antitrochanters.  
·· From proximal articular surface, not including cnemial crests.  
†† Midline of ventral surface of synsacrum.  
‡‡ Through antitrochanters.  
§§ From pro-maxillary articular surface, not including coronal crest.

1996:105). The hindlimb elements of the Wake Island Rail, as typical of most flightless rails, are more robust than in comparable volant species (Fig. 5).

Weight and Brain Volume.—No direct measurements of the weight of G. wakensis appear to have been taken prior to its extinction. Livezey (2003:98) extrapolated a weight of 113 g from

TABLE 3. Length measurements (mm) from skins of species of Gallirallus in USNM collections. The series of G. philippensis includes four males and four females from the Philippines, three males and five females from Celebes, and four males and four females from Palau. The specimens of G. owstoni were all wild-taken. Range with mean in parentheses ± standard deviation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wing chord</th>
<th>Culmen</th>
<th>Tarsus</th>
<th>Middle toe with claw</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. wakensis Male</td>
<td>80.1–97.4</td>
<td>24.9–29.4</td>
<td>33.0–36.9</td>
<td>36.7–40.9</td>
</tr>
<tr>
<td>n = 16</td>
<td></td>
<td>(91.1 ± 4.77)</td>
<td>(27.2 ± 1.26)</td>
<td>(34.8 ± 0.97)</td>
</tr>
<tr>
<td>G. wakensis Female</td>
<td>75.8–93.8</td>
<td>22.7–25.4</td>
<td>32.2–34.9</td>
<td>35.7–47.7</td>
</tr>
<tr>
<td>n = 15</td>
<td></td>
<td>(87.7 ± 5.07)</td>
<td>(24.2 ± 0.9)</td>
<td>(33.2 ± 0.64)</td>
</tr>
<tr>
<td>G. philippensis Male</td>
<td>129–144 (136.3)</td>
<td>26.5–34.4 (30.5)</td>
<td>40.5–44.9 (43.3)</td>
<td>40.5–45.6 (42.9)</td>
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<tr>
<td>n = 11</td>
<td></td>
<td></td>
<td>n = 12</td>
<td>n = 12</td>
</tr>
<tr>
<td>G. philippensis Female</td>
<td>125–140 (131.3)</td>
<td>27.5–31.5 (28.8)</td>
<td>39.0–43.7 (42.1)</td>
<td>37.1–44.2 (43.4)</td>
</tr>
<tr>
<td>n = 12</td>
<td></td>
<td></td>
<td>n = 11</td>
<td>n = 12</td>
</tr>
<tr>
<td>G. owstoni Male</td>
<td>124–126 (125)</td>
<td>34.1–41.9 (38.9)</td>
<td>46.7–53.2 (51.0)</td>
<td>43.1–50.3 (47.5)</td>
</tr>
<tr>
<td>n = 5</td>
<td></td>
<td></td>
<td>n = 5</td>
<td>n = 5</td>
</tr>
<tr>
<td>G. owstoni Female</td>
<td>110–115 (112.2)</td>
<td>33.4–35.1 (34.1)</td>
<td>46.2–49.4 (47.5)</td>
<td>44.1–46.1 (45.1)</td>
</tr>
<tr>
<td>n = 5</td>
<td></td>
<td></td>
<td>n = 4</td>
<td>n = 2</td>
</tr>
</tbody>
</table>
measurements of femora and tibiotarsi. Iwaniuk et al. (2004) estimated weight of one individual at 99.2 g based on ratios derived from skeletal measurements. They found that the predicted brain volume based on that calculation was 1.26 ml whereas the actual brain volume was 1.45 ml.

**Sexual Differences.**—There is an apparently skewed sex ratio among the USNM series, which comprises 28 males versus 17 females. There are only four specimens (2 males and 2 females) with sex reported in other collections. This could be due to collecting bias with males being more aggressive and conspicuous and females being more retiring, which is also suggested by the condition of the primaries. Twelve of the males (43%) had the primaries so worn and broken that wing chord could not be measured, whereas among the females only one was in such condition. We rated the primaries in the male series as being relatively unworn (4), some new but others worn (1), intact but outer vanes faded (7), or broken (12). The majority of females (11) had the primaries intact but faded and three had
what appeared to be new primaries. Abrasion against vegetation is probably the cause of this degradation of the primaries; apparently males were more territorial than females and spent more time chasing other males through the scrub.

Males of *G. wakensis* are distinctly larger than females (Tables 3, 4; Figs. 6, 7), as typical of many species of rails. Analyses of coefficients of variation, however, show that neither males nor females are more variable than the other (S. J. Parry, pers. comm.). The size difference does not hold for the wing and pectoral elements, however, which are nearly identical between males and females. There may have been selection for relatively larger wings in females, which presumably had at least as much responsibility for care of young as males, because the wings were used in threat postures against potential predators of eggs and young such as hermit crabs and rats.

**Additional Measurements.**—Tail measurements were not included (Table 3) because tails of the *Tanager* series of *G. wakensis* are extremely abraded or completely molted, making measurements almost useless. Tails of six relatively intact specimens ranged from 37.0 to 40.2 mm (mean = 38.3). Tail lengths in two less worn males in other collections were 42.5 and 43.0 mm and in the unsexed lectotype, 36.3 mm.

The following measurements are from the three complete skeletons and are included for potential comparison with new species of *Gallirallus* that may be found in the fossil record of Pacific islands. The first two are males and the third is a female. Mandible: symphysis length 7.1, 7.0, and 6.1 mm. Humerus: shaft width at midpoint 1.9, 1.9, and 1.7 mm; distal width 5.1, 5.3, and 4.8 mm. Carpometacarpus: proximal depth 4.3, 4.6, and 3.9 mm. Tibiotarsus: minimum shaft width 2.5, 2.5, and 2.4 mm; distal width 5.8, 5.7, and 5.2 mm. Tarsometatarsus: proximal width 6.3, 6.1, 5.7; shaft width at midpoint 2.8, 2.9, and 2.5 mm; distal width 6.4, 6.4, and 6.0 mm.

**Molt.**—Only two of the 10 AMNH Owston specimens taken at an unknown time of year have reasonably unworn primaries. Most of the rest have the primaries broken and are variably bleached and worn. The tail is partly or completely absent in four specimens. Wetmore’s measurements of this series included the tail, and the four specimens that we considered to have the tail worn or absent have the smallest measurements; perhaps Wetmore was measuring coverts, rather than rectrices. The birds in the *Tanager* series, except for the very abraded specimens, are mainly in fairly fresh plumage but more faded than those collected in June by Spencer and Garlough. Some individuals have very worn feathers on the back of the head and the lower back, suggesting the mantle and forecrown were renewed first. One female is distinct in having the foreparts in fresh plumage (forward of the pectoral band ventrally, a little farther back having the foreparts in fresh plumage; perhaps Wetmore was measuring coverts, rather than rectrices. The birds in the *Tanager* series, except for the very abraded specimens, are mainly in fairly fresh plumage but more faded than those collected in June by Spencer and Garlough. Some individuals have very worn feathers on the back of the head and the lower back, suggesting the mantle and forecrown were renewed first. One female is distinct in having the foreparts in fresh plumage (forward of the pectoral band ventrally, a little farther back dorsally) but the wings and the rest of the back, breast, and belly are extremely worn and faded. The tail is partly or completely absent in four specimens. Wetmore’s measurements of this series included the tail, and the four specimens that we considered to have the tail worn or absent have the smallest measurements; perhaps Wetmore was measuring coverts, rather than rectrices. The birds in the *Tanager* series, except for the very abraded specimens, are mainly in fairly fresh plumage but more faded than those collected in June by Spencer and Garlough. Some individuals have very worn feathers on the back of the head and the lower back, suggesting the mantle and forecrown were renewed first. One female is distinct in having the foreparts in fresh plumage (forward of the pectoral band ventrally, a little farther back dorsally) but the wings and the rest of the back, breast, and belly are extremely worn and faded. interspersed with a few new feathers on the flanks and belly. The rump feathers also appear new. This entire series appears to be in tail molt or to have the rectrices worn away. Lyons remarked on birds with sandy or straw colored primaries, which is how they appear when worn and very faded. He noted only one of 60 birds in this condition on 9 June but that the number had considerably increased by 25 August (Lyons 1939). A specimen in completely fresh plumage

### TABLE 4. Measurements (mm) from trunk skeletons of Wake Island Rail (*Gallirallus wakensis*). Those from the three complete skeletons of *G. wakensis* (Table 2) are also included. Range with mean in parentheses ± standard deviation. Measurements taken as described in Table 2. Shaft width of femur is at midpoint.

<table>
<thead>
<tr>
<th>Measurement</th>
<th><em>G. wakensis</em> males</th>
<th><em>G. wakensis</em> females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humerus proximal width</td>
<td>6.6–7.4 (7.0 ± 0.25) n = 11</td>
<td>6.1–7.2 (6.8 ± 0.50) n = 4</td>
</tr>
<tr>
<td>Coracoid length</td>
<td>15.7–17.7 (17.1 ± 0.53) n = 18</td>
<td>16.2–16.6 (16.4 ± 0.13) n = 10</td>
</tr>
<tr>
<td>Sternum length</td>
<td>23.2–27.3 (25.6 ± 1.88) n = 19</td>
<td>23.0–27.0 (25.2 ± 1.09) n = 10</td>
</tr>
<tr>
<td>Sternum depth</td>
<td>5.4–8.0 (7.0 ± 0.64) n = 19</td>
<td>6.3–7.7 (7.1 ± 0.48) n = 10</td>
</tr>
<tr>
<td>Pelvis length</td>
<td>29.0–32.9 (31.3 ± 1.02) n = 19</td>
<td>25.8–31.5 (30.1 ± 1.58) n = 10</td>
</tr>
<tr>
<td>Pelvis width</td>
<td>16.8–18.0 (17.4 ± 0.39) n = 19</td>
<td>15.9–18.0 (16.5 ± 0.37) n = 10</td>
</tr>
<tr>
<td>Femur length</td>
<td>36.3–39.1 (37.9 ± 0.71) n = 19</td>
<td>35.6–36.7 (36.1 ± 0.41) n = 10</td>
</tr>
<tr>
<td>Femur proximal width</td>
<td>6.6–7.5 (7.1 ± 0.23) n = 19</td>
<td>6.4–6.9 (6.8 ± 0.15) n = 10</td>
</tr>
<tr>
<td>Femur shaft width</td>
<td>2.9–3.3 (3.0 ± 0.10) n = 19</td>
<td>2.6–3.0 (2.8 ± 0.13) n = 10</td>
</tr>
<tr>
<td>Femur distal width</td>
<td>6.7–7.6 (7.0 ± 0.20) n = 18</td>
<td>6.1–6.8 (6.6 ± 0.21) n = 10</td>
</tr>
</tbody>
</table>
with unworn primaries from November 1935 (BBM) has the tail present and distinct.

**BEHAVIOR**

**General Demeanor** (Figs. 8, 9).—Wetmore (1970:2) encountered the birds "singly, or two or three in loose association." "The birds were alert and inquisitive and came walking out with head and neck erect and jerking tails. Though not averse to crossing open spaces, they walked ordinarily under cover, apparently through a desire to keep out of the intense rays of the sun. Often while sitting down one came within three or four feet of me peering curiously with outstretched neck and jerking tail while it uttered a low cluck. Though tame they took care to keep well out of reach, although I did knock one over with a slight switch. Rails were much shyer..."

during the rain" (Wetmore in Olson 1996:105); "About fifteen rails were seen [3 August] at different times in the shrubbery or at the edge of the Sesuvium. They ventured out ten or twelve feet from the edge where they walked about unconcernedly so long as I was quiet, but skipped rapidly to the protecting shelter of low growing trees at any suspicious movement. Ordinarily their motions are deliberate...Should one chance to see me before I call, it seems greatly startled and with head erect runs swiftly away, dodging behind stumps or other cover until far beyond reach. Pursuit at such times is useless as the birds travel rapidly under the thick cover where they may not be seen. As they walk about, the tail is held down but at short intervals is jerked over the back. Though they come within three or four feet of me in the heavy brush, I find it difficult to get pictures
of them as they are always concealed by a screen of twigs” (Wetmore in Olson 1996:111). The experience of Spencer (1936) that the rails could easily pass through 50-mm mesh indicates they could also squeeze through interstices in vegetation that size or smaller.

“The species has much personality, being serious business-like little birds...they look like Hungarian Partridge [Perdix perdix] and act like chickens” (Lyons 1939, June). “Wake Island rails, larger than those of Midway, ran about here and there, but not underfoot. Here at Wake, they give a definite impression of barnyard fowl” (Miller (1936:694). “The bird compares in size to the three weeks old baby domestic chicken” (Spencer 1959).

Rat control biologists, operating mainly on Peale Island in 1936, were concerned about the effect that poisoning might have on the rails. “One full day was given over to making an old chicken pen, rail escape proof. The pen was originally constructed with Standard Chicken Wire [2 inch = 50 mm mesh] and from sad experience it was found that the rails could squeeze through this size of mesh wire. Our only salvation was in boarding up the sides high enough to prevent the rails from jumping over. One full day and one evening was spent attempting to catch rails with the use of traps, nets, and flashlights, but to no avail. Only 15 birds were caught. It was quickly decided that our plan calling for the corralling of the rails, before placing the poison bait in the field was going to be entirely unsuccessful, as in order to corral 4-500
FIG. 8. Postures assumed by the Wake Island Rail (Gallirallus wakensis). Expertly detailed by Julian P. Hume from photographs by Torrey Lyons that were too small or indistinct for other reproduction.

birds at that rate would take a month’s time” (Spencer 1936:6). Rat poisoning appeared to have had no effect on the rails and the “fifteen rails penned during the program were liberated at the close of work” (Spencer 1936:7).

Vaughn (1945:27-28) made the following observations on the rail in April 1938: “They travel around with, and even eat from the same dish with, the small vegetation-eating rats that infest the island. Long unacquainted with human beings and therefore unafraid, they have become quite friendly with our men during the three years the Pacific Airways have occupied the island. They stand by dozens on the steps of the hotel kitchen door, peering thru the screen at the staff and going crazy with delight when one of the Chinamore [Chamorro] kitchen-boys (natives of Guam) comes out with scraps for them. They walk over his shoes and jump high in the air, just like young chickens at feeding time. During the heat of the day, they get under the hotel or go down into the rat burrows to keep cool; at night, they go foraging abroad with the rats.” We would guess that such nocturnal foraging as witnessed by Vaughn probably occurred mainly under artificial lighting, although some natural nocturnal foraging by rails may be assumed if they fed regularly on the largely nocturnal hermit crabs.

Locomotion.—Lady Hay Drummond-Hay (1939:337), famed for her adventures in zeppelins, was so enchanted with Wake that she stayed there for 2 weeks in 1939 and noted “flightless rails with no air-bearing wings, which run along the ground, comically like a well-trained motorist indicating his direction right or left by extension of the appropriate wing.” Vaughn (1945:28) reported that: “They do not like to be handled however and when the men chase them, they stretch their useless stubby wings to balance themselves and run with the speed of a Bobwhite [Colinus virginianus].” “Practically the entire life of the bird is spent on the ground, only occasionally do they get up into low trees and bushes by the jump-step climbing method” (Spencer 1959).

Lyons (1940), in general notes without specific dates, observed the rails did not fly, although he had seen them flap their wings to aid in running when very frightened or when scared by a noise. The rails, when walking, make a succession of quick steps, then pause for observation, poised in cautious approach, a definite poised pause be-
between each step. One that was feeding on insects in a Cordia bush 60 cm off the ground fluttered its wings to keep balance and as an aid in climbing. Another in jumping off a 4 foot (1.2 m) high box, flapped its wings to break the fall.

Spencer (1936) found the birds could not escape from pens that were higher than they could jump. “One running very fast flapped its wings hard and appeared to be taking most weight off [with its?] wings” (Lyons 1939, 12 Jul). “Another one running seemed almost to take off” (Lyons 1941, 2 Apr).

Home Range.—“The birds seem to have very limited ranges” (Wetmore in Olson 1996:111). “These birds seem very sedentary. Those that I take on sandy areas where there is only scattered areas of shade, are very worn and pale color above, those from certain sections where there are extensive dead-falls have the wing feathers worn and abraded, apparently from their use in climbing about. This is true though more suitable areas where conditions are less severe may be found near at hand” (Wetmore in Olson 1996:184). Lyons noticed one that was missing a foot and was not seen >15 m from the greenhouse on Peale Island, and another that was marked with blue paint was seen once by the recreation hall and three times by the greenhouse (Lyons 1939, 26 Jun).

Vocalizations.—“They utter a low chattering call, a chattering note that is easily recognized as a rail call and also a low cluck that is audible only when near at hand” (Wetmore in Olson 1996:105). “When I squeak they reply with a rattling chatter that is unmistakably a rail call and come running toward me under the brush. Near at hand they give a low clucking call” (Wetmore in Olson 1996:111).

Newly hatched downy young made loud wails while the adults attending them made complaining sounds (Lyons 1939, 23 Oct). An adult circling away from its young that it perceived to be under
threat cackled slightly (Lyons 1939, 13 Jun). Two-thirds grown young did a lot of peeping (Lyons 1939, 26 Jun).

Aggression.—Lyons frequently noticed the rails fighting. “They crouch and cackle and purr and slice in sideways or jump up like fighting cocks. Usually one stands and the other beats an honorable and deliberate retreat” (Lyons 1939, 18 Jul). “One bird defending a nest advanced in defiance, feathers on back and sides up, wings out, head low” (Lyons 1939, 18 Sep).

Interaction with Rats.—Lyons (1939, 29 Jun) noted one rail that contested a food object that a full grown rat was dragging—each respected the other. The rail’s most effective ruse was a shaking of the wings upon which the rat retreated 2 feet (0.6 m). The rail was apparently not overly interested and left after a minute. Lyons (1940, 3 Sep) found no instance of rails touching a dead rat nor saw any evidence of rails eating dead rats from the poisoning program of 5 July. Vaughn (1945) reported that the rails fed together with rats and even resorted to rat burrows to escape the heat of the day.

Feeding.—“In feeding they dig up leaves and soil with a quick thrust of the head in search of shells or insects” (Wetmore in Olson 1996:105). “...they pause frequently to dig with sidewise thrusts of the bill in the loose soil to expose shells, insects or other desirable food” (Wetmore in Olson 1996:111). “The chief enemy of the hermit crab is a small ground bird known as the wingless [sic] rail,...a meek-looking little chap, a doughty fighter. I saw one attack a crab with an approach so rapid that the crab did not have time to clew up in his shell. The rail led to the crab’s chin like lightning several times and it was all over for the crab. Whereupon the rail and his friends proceeded to eat the hermit” (Grooch 1936:115-116). One of Grooch’s photographs (Fig. 10) shows “a wingless rail attacking a hermit crab.”

“The birds were observed to feed on seeds, insects, small lizards, and on the soft parts of the hermit crab. They were terrestrial, only occasionally climbing into low bushes, and were almost flightless. The abundant rat and the myriad of hermit crabs were reported as predatory to some extent on the eggs and young of the rail. The crabs and rats were efficient scavengers, recorded as feeding on the bodies of dead birds and attacking sickly ones. In turn, the rails kept watch as the crabs changed abode from outgrown shells that served as their protective shelter. As the soft bodies of the hermits were exposed, these were
attacked and the animals killed and eaten” (Wetmore 1970).

Lyons (1940, 3 Sep) noted the rails did not scratch with their feet, but would instead flip with the bill. One feeding in dry crinkled leaves under a Heliotropium used the bill most effectively in scratching with about three rapid flicks in a series, throwing the leaves about 30 cm (Lyons 1939, 1 Aug). One rail dug with the bill for grubs in loose coral soil in a hole as big as the rail’s body [60 mm deep], as another stood patiently by and also grabbed food as it was dug up, the digging bird had tan tipped plumage [presumably remiges] whereas the waiting bird was in fresh plumage (Lyons 1939, 16 Sep). Rails were seen feeding on insects for which they climbed up in bushes, and Lyons mentioned adults carrying caterpillars that were evidently intended to feed to the young. Lyons found caterpillars of the noctuid moth Achaea janata, a species widespread in the tropical and subtropical Pacific and Australia, on Wake Island where they were feeding on Cordia and also on tomato plants (Williams 1945). The rails fed eagerly on human food scraps and also on spilled chicken feed (Lyons 1939, 26 Jun; Vaughn 1945).

Drinking and Bathing.—Wetmore (1970:3-4) noted that “there were no permanent pools of fresh or brackish water on the atoll. Storm blown materials over the land surface, however, included abundant hand-sized shells of a bivalve mollusk of the genus Tridacna. It was fairly common to find these with the concavity facing up. The rains that fell daily during our stay (Jul-Aug 1923) kept these filled with fresh water, and to these the rails came very frequently to drink. This, however was not a permanent supply, as in the history of Wake since it became an airport, extensive periods of drought are recorded. In studies of the abundant Polynesian rat in this subsequent period it was found that in dry periods these mammals sought the large immature calyces of the abundant wild morning-glory Ipomoea tuba as a supply of fluid in place of water. It may be assumed that the rails also did this.”

“While testing the well on Peale we pumped five or six hundred gallons of water out on the ground where it formed a large shallow puddle. Dozens of rails took advantage of this opportunity to have a bath. They splashed about and appeared to enjoy themselves hugely” (G Groech 1936:115–116).

Breeding (Figs. 4, 9).—“The birds are now [28 Jul 1923] in breeding condition and Bryan noticed a pair in copulation today” (Wetmore in Olson 1996:105). “They are fairly fat and in good condition. The breeding season is at hand as males have enlarged testes and in some females the oviduct shows development. None seem to have laid as yet [3 Aug 1923]” (Wetmore in Olson 1996:105). We examined a fluid-preserved specimen taken on 29 July 1923 in which the right testis was 5.8 x 13.9 mm and the left testis 6.0 x 12.5 mm. Given shrinkage due to dehydration in alcohol, the dimensions would have been even greater in life, and Wetmore’s assessment that the testes were enlarged is confirmed.

There is no sign of birds in recognizably juvenile plumage among the 39 skins at the USNM from the Tanager Expedition (late Jul to early Aug). One would expect at least a few birds from the previous nesting in a series this large and if they had molted from juvenile plumage by late summer, it would indicate possible hatching about April.

“During the last part of August [1936] a number of broods of rails were hatched, and at the completion of the rat control work in September, these same broods and later ones were still roaming the poisoned area in full strength” (Spencer 1936:7). The only known specimen in juvenile plumage (USNM 365254, Frontispiece) was collected on 7 June 1937 and was probably at least 3 or 4 weeks of age, indicating hatching in the early part of May. “Two broods a year seem to be the rule, one appearing in April to May, the other August to September” (Spencer 1959).

Lyons (1939) noted a young bird at end of down stage on 13 June. Young two-thirds grown were present on 26 June (Lyons 1939). Four downy young obtained on 21 July 1939 (MVZ) were newly hatched (Fig. 3B). A just hatched chick in the chicken yard, wobbled, black down, no adult in sight (Lyons 1939, 25 Jun). Three two-thirds grown young around the quarters on 26 June (Lyons 1939). Four young in a group on 12 July (Lyons 1939). Rails very excitable for the last few weeks (young presumably hatching) and a half grown one seen on 7 and 10 October (Lyons 1939). Two newly hatched young with five adults on 23 October (Lyons 1939). In about a week from the first hasty rail, six had been hatched—three near the hotel and three near the greenhouse. I believe more have been hatched since (Lyons 1939, 12 Nov). Following the nest that hatched on 20 July, young were seen that indicated about five other hatches on Peale. On 20 August these babies
were almost as tall as adults but still had very few hard feathers, grey (Lyons 1940, 3 Sep).

Nest and Eggs.—"The nest is constructed on the ground as saucer-like depressions in areas of dense ground cover. One to three camouflage speckled eggs are laid" (Spencer 1959). Lyons' photographs (e.g., Fig. 4A) show that the eggs were ovate and speckled; a rough estimate based on comparisons of chick size and human finger size suggests the eggs of *G. wakensis* may have measured about 20 x 30 mm, which is smaller than the various measurements given for *G. philippensis* (Taylor 1998). Vaughn (1945:27-28) found the rails nesting on bare sand at the base of the scrubby beech [sic] magnolias [*Heliotropium*] in April 1938, laying a clutch of four or five eggs, judging by the number of young in the nest. Lyons (1939, 16 Sep) discovered two nests side by side under low *Cordia* bushes. There were many eggs and maybe two birds on each nest as three flushed and one remained. Lyons was certain that two birds were on the nest on which the one bird remained. Two days later there were three nests where there were two before, each with 6, 3, and 7 eggs, respectively. At least five birds were in attendance at the nests. A few twigs and leaves were over the backs of the birds as they sat on the nests (Lyons 1939, 18 Sep). Two days later (20 Sep) the eggs and birds were gone.

On Peale Island the "(day after brush where birds lived cleared away—no nests seen—between Old & New Hydroponicum and Circle). Bird with egg in mouth motions as if it would pick it up but [put?] egg on ground. Bird saw me and left. In a few minutes I sneaked back to see if bird had returned—egg gone, no sign of egg, bird or nest within 20 ft [6 m]." (Lyons 1939, 5 Oct).

Parental Care.—"There is an indication that young of several hroods are brought together and the parent birds sharing the responsibility of caring for the group as a whole. The young nestlings are similar to domestic chickens in being able to forage for themselves soon after hatching" (Spencer 1959).

An adult and a young bird, end of down stage, and the adult left the young, which moved straight away from my approach and into cover (shush). The adult circled around, cackling only slightly to 30 feet (10 m) from where it left the young (Lyons 1939, 13 Jun). Newly hatched young (2 attended by 5 adults) moved very rapidly with a creeping motion, while the adults stood around and complained and warned the young who scurried away, keeping under cover (Lyons 1939, 23 Oct). "Caught a small rail at end of walk front of south wing of hotel, froze under some *Boerhaavia diffusa* (a mat like growth). I lay down with the young bird in my hands and watched the mature birds, which came within 3 ft [1 m], only one, possibly the mother, made a menacing gesture by advancing in a hunched position with the wings held open and slanted backwards. Six adult birds gathered as the little one cheeped constantly." (Lyons 1939, 26 Oct). Saw young still in down unaccompanied by adults (Lyons 1939, 12 Nov). Flightless rail very busy now bringing up young (Lyons 1939, 13 Nov). Latest baby seen in last day or two is about 4 days old—single nurse (Lyons 1939, 19 Nov). About as many young as adults—none in down—mostly half weight, stand 2/3 as high, a dull buff grey. Today watched two young heckle their nurse: peeped, butted into her, pulled at her feathers (acted like a calf when still hungry and no milk flowing). The nurse was unruffled and ran away half-heartedly with the young at its heels, butting and pulling feathers (Lyons 1939, 29 Nov). Babies apparently all grown up, some look young but not under supervision and have adult type plumage (Lyons 1940, 10 Feb). At the PAA compound discovered rail nest in chicken yard, under *Cordia* but no ground cover. In the single nest, the chicks were nearly all hatched at 5:30 PM. Three eggs were left, and the nurses had babies away as far as 30 ft [9 m] about 7 were in the nest, about six with nurses—2 babies dead (Lyons 1940, 20 Jul). At the PAA compound at noon the three extra eggs had been hatched, only 2 young were in nest and the rest were scattered over the chicken yard with about 7 nurses—2 more had died (Lyons 1940, 21 Jul). By today there were no babies left in the chicken yard and all were out under a patch of *Cordia* across the road and south (Lyons 1940, 24 Jul). Rails seen running toward *Cordia* patch with caterpillars to where babies stay (Lyons 1940, 29 Jul).

Synthesis of Phenology, Cooperative Breeding, and Molt

All known specimens of Wake Island Rail, except those of unknown date collected in 1892, were taken from June through November (Table 1). Thus, we have information on molt and breeding from only half of whatever cycles to which the species may have been subject, which may not have been strictly annual. Lyons'
observations indicate that young grew to near the size of adults in a month and were apparently indistinguishable from adults in less than 10 weeks. Birds were not yet breeding at the end of August or the beginning of September 1923 and no birds showed signs of juvenile plumage. Thus, if they had bred earlier in the year, hatching would probably have been in April or May. This could fit with Spencer’s impression that rails bred in April to May (supported by his nearly adult-size specimen from 7 Jun) and again in August to September when hatchlings were seen. Vaughn noted nests in April 1938. However, Lyons (1939) observed birds almost out of down on 13 June, just hatched on 25 June, downy on 25 July, eggs on 16 September and 5 October, newly hatched on 23 October, more hatching beginning in November, and ~4 days of age on 19 November. Eggs and downy young are not mentioned again until 20 July 1940. Thus, there seems to have been egg-laying throughout 1939 and well beyond the time of year in which the rails did not breed at all in 1923 and were evidently not breeding in 1936–1937. Thus, the breeding season was probably influenced by environmental conditions such as drought, when breeding may not have occurred.

The Wake Island Rail appears to have had a most unusual communal breeding system with up to three nests being placed together and nests apparently tended by more than two birds per nest. Young were attended, defended, and fed by groups of adults until well after hatching. This would presumably have been an effective way of deterring predation on eggs and young by hermit crabs and rats. Breeding seasons were at times irregular, or spread over 5–6 months. At least small groups of females would have to be capable of synchrony in laying that did not coincide with that of other groups of females, as apparently was the case in 1939, for communal breeding to be maintained. Unfortunately, it is not known whether males participated in this communal breeding pattern.

We know less about the phenology of molt. Birds from the Tanager collections (Aug-Sep) are mostly extremely worn and faded. Lyons observations of “straw-colored” primaries, which is their appearance when faded and abraded, included only one of 60 on 9 June 1939, but such individuals had become more numerous by August, in agreement with the Tanager specimens. The only available adult in fresh plumage was taken in November and the little available evidence suggests a full body molt in September–October.

**POPULATION SIZE AND POTENTIAL SOURCES OF MORTALITY**

*Abundance.*—Wetmore (1970:4) noted that his collecting of specimens of the rail “was so distributed as not to bring undue pressure on the birds from any one area. Their abundance was shown when on my last day, in one limited space around a small opening, I counted 15 individuals.” That was evidently 3 August 1923 when his journal mentions “about” 15 rails (Wetmore in Olson 1996:111), of which he collected eight, although the expedition did not leave until 5 August. Wetmore collected eight rails on Wake Island itself on each of the following days: 28–29 July, 1 and 3 August. Six were taken on Wake on 2 August and eight were taken on Peale Island on 30 July.

The rat control team of 1936, when faced with the impossible task of capturing all the rails on Peale Island prior to poisoning operations, estimated there were 400 to 500 birds on Peale alone (Spencer 1936). Later, Spencer (1959) estimated the total population of the rail at a “few hundred” individuals. “The majority of the birds are found on the islet of Peale. Small scattered groups inhabit Wake and Wilkes Islets” (Spencer 1959). This is the only possible indication that rails were ever found on Wilkes and, if true, they may have arrived there as a deliberate introduction. The fact that there were only “small scattered groups” on Wake Island proper in the late 1930s possibly indicates that the reduction in habitat caused by the construction of the airstrip may have had a negative impact on population size.

Lyons (1939, 9 Jun) observed a flock of 60, by count, at the chicken feed storage shed on Peale and there was still a large flock by the greenhouse on 26 June. Many were seen on Wake in the meadow along the lagoon shore on 2 April—especially the meadow at the tip of the lagoon and many were heard calling (5 calls, 20 birds seen). (Lyons 1941).

*Direct Observations of Mortality.*—Lyons mentioned several instances of rail chicks dying shortly after hatching but the causes of their deaths were unknown. Perhaps hyperthermia caused by exposure of small, black chicks to the harsh heat and sun of Wake Atoll may have been
involved. With the onset of human occupation of the island, vehicular traffic became a source of mortality. Lyons' only adult specimen was a female found on Wake Island proper that had been run over by a truck, which provoked the very curious comment that the "wing bone [presumably the humerus, was] only about 1/4th as resistant to fracture as leg bones" (Lyons 1939, 25 Oct). Scientific collecting accounted for 66 additional specimens over a period of nearly 50 years with the 46 removed in 1923 having clearly had no influence on population size as evidenced by the abundance of the species in the late 1930s.

Possible Mortality from Inundation.—Beginning with the U.S. Exploring Expedition (1841), visitors have remarked on the evidence of the effects of high seas on Wake Atoll. "From appearances, the island must be at times submerged, or the sea makes a complete breach over it; the appearance of the coral blocks and of all the vegetation leads to this conclusion, for they have a very decided inclination to the eastward, showing also that the violent winds or rush of the water, when the island is covered, are from the westward" (Wilkes 1844:285). The expedition's naturalist, Titian Peale, also noted that "the only remarkable part in the formation of this island is the enormous blocks of coral which have been thrown up by the violence of the sea" (Pocsch 1961:199). Wetmore noted on Wake Island in 1923 that "huge blocks of a consolidated conglomerate of coral and coral sand have been thrown up at intervals, some of them from eight to fifteen feet in diameter" (Olson 1996:105). In exploring the atoll in 1935, Grooeh (1936:92–93) found that Wilkes Island "was no place to build an air base because it showed plain evidence of having been underwater. [There were] logs in the center of the island that could only have been washed up by the sea. In many places driftwood was lodged in the trees overhead." Yet it "was at once apparent that Peale Island was a different place altogether from Wilkes Island. There were no rocks and the soil was a rich brown loam. There were fair sized trees and many vines, and no evidence whatever that the island had been under water."

There is little doubt that inundations by the sea had an effect on mortality of the rails. Wetmore noted that Wilkes had apparently borne the "full brunt of the typhoon that swept the atoll. Large trees were entirely destroyed" and "strangely enough no rail have been found in Wilkes Island though the birds are common on Wake Island across a narrow channel" (Olson 1996:108). Flightless rails swept out to sea in a storm would most likely have drowned or been eaten by predatory fish.

Possible Mortality from Predators.—Wetmore (1970:4) accurately summarized the potential for predation on the rail: "The rat mentioned and a hermit crab that swarmed on the island would appear to have been the only predators that might have affected the rails. But, from their abundance, the birds seemed to encounter no serious difficulties." Miller (1936:694) mentioned in December 1935 "a never-ending battle between the flightless rails, the rats, and the hermit crabs. Constantly they prey on one another." This was certainly an exaggeration. Atkinson (1985) hypothesized that, because of their interactions with land crabs, birds on Pacific islands relatively near the equator may have developed behaviors that allowed them to cope better with the subsequent arrival of rats. We know that rails certainly preyed upon hermit crabs and rats may have also, but the cooperative breeding system and apparent intense parental care of the rails would have prevented much interference with eggs and young by crabs or rats.

Rats, however, have frequently been implicated in the extinction of the Wake Island Rail. The Pacific rat was doubtless transported to Wake by prehistoric voyagers and its presence was first noted by the U.S. Exploring Expedition in 1841, by which time the rat may already have been on Wake for centuries. Several observations quoted indicate that in the 1930s, Wake Island Rails co-existed with rats. Led alongside them, resorted to rat burrows to escape from sun and heat, and that rails and rats were mutually "respectful" of one another in disputes over food. Human settlement brought an increase in food to be found by rats in human habitations and refuse dumps, and doubtless resulted in increased population size of rats, but there is no evidence this had any deleterious effect on populations of rails.

Vaughn (1945:27–28) considered the rats on Wake in 1938 to be "vegetation-eating." Following the war, Fosberg (1959) reported the observations of Fred Schultz who was in charge of pest control on Wake for the Civil Aeronautics Administration. Rats had been reported in sleeping quarters and a dining hall, but Schultz "found that they lived largely in the clumps of bushes, especially those which were covered by tangles of the wild white morning glory, Ipomoea tuba." He found they used the enlarged immature fruiting
calyces of this species in lieu of a water supply (Fosberg 1959:7). This behavior would be expected of *Rattus exulans*, which had centuries to adapt to conditions on Wake Island, rather than a commensal such as black rats (*R. rattus*). If rats of European origin (*R. rattus* or Norway rat, *R. norvegicus*) got onto Wake Island, this would have occurred during or after World War II and their presence on the island has been claimed repeatedly. The first biologist to assess Wake after the war was A. M. Bailey, who was ashore in mid-May 1949. He was the first to report the extinction of the Wake Island Rail and wrote that rats “or possibly the starving Japanese troops themselves, may have exterminated them” (Bailey 1951a: 36). He further stated that during “the Japanese occupation of Wake in WW2, *Rattus rattus* was introduced with devastating effects on the bird-life....As these rats were present after the war, their import must have occurred during Japanese times.” Bailey may have been proceeding on the assumption that the situation paralleled that on Midway Island, which he had also visited, and where *Rattus rattus* introduced during WW II did exterminate the healthy introduced population of Laysan Rail (Olson 1999b). His identification of the Wake Island rats may be doubted, however, as he does not mention *R. exulans*.

Atkinson (1985:40) attributed *R. exulans* to Wake on the basis of Peale’s (1848) report and inferred the introduction of *R. rattus* in the period 1923–1951 from Bryan (1943 [sic = 1942]), Fosberg (1959b), and King (1973). Bryan, however, makes no mention of anything that could be interpreted as *R. rattus* but only what is clearly *R. exulans*. It is not at all clear upon what King (1973:101) based his statement that on Wake Island: “Feral cats *Felix catus*, black and Polynesian rats occur on all three islets.” Fosberg (1959:7) encountered only a single rat in 1953—“a large blackish one,” but his informant Schultz considered there were four kinds of rats on Wake Island. Bryan (1959:8) in evaluating that assessment stated that all available specimens of rats from Wake were *R. exulans* and that a “series of skins and skulls collected to represent the rat populations living on the island would be very desirable to settle this question.”

Bryan was correct that all available specimens of rats from Wake have been identified as *R. exulans*, including those from the 1923 Tanager expedition (USNM, BBM) and all those obtained by Kentler and other Pan Am employees in 1935 and 1936 (BBM). Trapping that has occurred since cat eradication programs began in 1996 confirmed that the only rats on Wake Island were *R. exulans* until the Asian ship rat (*R. tanezumi*) was trapped on the island in 2007. That species is believed to have “arrived during the mid-sixties with Vietnamese refugees” (Rauzon et al. 2008a:13).

It is possible that either of the widespread European commensal species of rats may have been introduced to Wake Island and were subsequently exterminated by cats, but this would almost have to have been in the years after the war and it seems unlikely because both *R. rattus* and *R. norvegicus* are larger, more aggressive species that usually supplant and even prey on *R. exulans* (Harper and Veitch 2006). Therefore, given the long period of co-existence of the Wake Island Rail with *R. exulans* prior to the war, we do not believe that rat predation was a factor in the extinction of *Gallirallus wakensis*.

**EXTINCTION**

The rail was such an unusual and conspicuous element on Wake that it did not escape mention in accounts of military officers on the island prior to the war. Devereux (1947:22–23), the commander of the U.S. Marines on Wake Island, wrote: “there was one weird bird I believe is peculiar to Wake. It was the flightless rail, which looked to me like a tiny cousin of the New Zealand kiwi. I do not know how he ever got to Wake because he can’t fly.” Bayler (1943:21), another officer under Devereux, mentions that: “I studied the little red-eyed ‘pee wee’ as it hopped about. The pee wee is a flightless bird, certainly a strange species to find fooling around an airfield. It is just a fluffy ball of feathers with no wings and no tail; the size of a robin, it is indigenous to Australia, and we used to speculate on how pee wees could ever have come to distant Wake Island.” The odd belief that the rail came from Australia goes back at least to 1935, as Grooch (1936:115–116) also alludes to an Australian origin. Bayler’s description of the rail is clearly the basis for the nearly identical characterization in Schultz (1978:114). Cunningham (1961:40), who was the Navy commander on the island contemporary with Devereux, also noted “a species of flightless rail no larger than a newborn chick.” Being flightless (and, as so often with flightless birds mentioned by nonscientific writers, described as “wingless”), the rail may have evoked some association...
with kiwis (Apteryx) of New Zealand, as suggested by Devereux, which may in turn have led to the vernacular name "peewee" and the belief that the bird originated somewhere to the south.

These three ranking military officers were among the last Americans on Wake Island who lived to tell their stories. Devereux having spent the entire war in a prison camp in China. As far as they knew, the rail was present and doing fine up until they were removed from Wake Island following the surrender of the island in December 1941. Years later, when queried about the possible former presence of albatrosses on Wake Island, Devereux responded: "To the best of my recollection we had frigate birds, tern and a small brown flightless bird, which I understand was peculiar to the island" (Devereux in litt. to C. E. Carlson, USFWS, 27 July 1959; Smithsonian Institution Archives, J. W. Aldrich Papers). This is further indication that as far as Devereux was concerned the rail was a living species up until December 1941.

The Japanese military occupied Wake Island in December 1941 and surrendered it in September 1945. During that period and for a good while afterwards, there was, understandably, no information at all regarding the natural history of Wake Island made available to the rest of the world. That did not inhibit speculation about what might be happening there. Less than a year after the Japanese occupation, Bryan (1942:214) predicted the demise of the Wake Island Rail: "It is not at all unlikely that this species has become extinct, due to the experiences through which the island has passed." Vaughn's notes (1945:27) on the birds of Wake Island were not published until June 1945, as the war still raged, but an editorial note remarked that "Mr. Vaughn's observations may well become a first and final chronicle, for the interesting birdlife of Wake may have become completely extirpated as a result of the Japanese occupancy." The nearly 4 years of Japanese occupation were marked by brutal deprivation and death by bombing and starvation. Habitat was destroyed to build barracks, revetments, air raid shelters and, eventually, for garden plots in attempts to grow food. Bombing removed additional habitat because as the war intensified, Wake became the target of hundreds of sorties, mostly carrier based, beginning in February 1942 and ending in August 1945 (Cohen 1983:77). This eventually made supply ships too vulnerable to stand off and ferry provisions to the troops; even attempts by Japanese submarines to float containers of food to shore at night proved unsuccessful. "In all, about 4,400 Japanese troops were stationed on Wake, but by the time of the island's surrender, deaths from air raids and malnutrion had reduced the number to 1,242" (Cohen 1983:77).

During the Japanese occupation, Wake Island was supplied mainly from Kwajalein Atoll, Marshall Islands, which fell to the U.S. in January 1944. Food rationing did not begin on Wake Island until May 1944, and rations were progressively reduced until reaching an all time low in July 1945. An attempt was made to supplement staples by growing vegetables and by fishing, but as fishing gear wore out and men weakened "the catch dropped to such a low level that it was not considered worth the effort. In addition to fish, some men caught and ate island birds, but the yield here also dropped in the last months, as men became weakened from malnutrition. Rats were also eaten whenever caught. The Japanese commanding officer, Admiral Sakibara, said that on one occasion the island garrison made a run on rats and in one single day killed 40,000 and ate them" (information from USSBS 1946).

Perhaps no place on earth would have been less suitable than Wake Island to sustain an isolated population of thousands of humans, whose numbers would certainly have been greater than the number of rails. If tens of thousands of rats were caught for consumption what chance did a few hundred flightless rails have? In addition to loss of habitat and direct predation, it is safe to speculate that, because of human disturbance, any semblance of successful breeding activity by rails would probably have been impossible. By war's end the rails were gone.

Greenway (1958:216) quoted a 1949 communication by station manager T. D. Musson to the effect that he had been familiar with Wake Island since 1946 and had never seen the rail. Bailey (1951a, b) searched for the rail unsuccessfully from 11 to 15 May 1949 and was told that none had been seen since the American reoccupation. "Rats, or possibly the starving Japanese troops themselves, may have exterminated them" (Bailey 1951a:36). "The war caused the destruction of the majority of the birds on Wake, including the unique flightless rails which were once so numerous, but apparently the Sooty Tern [Onychoprion fuscata] colony was protected so the birds would supply the starving soldiers with eggs" (Bailey 1951b:57).
Ripley (1977) noted Musson's surmise that the rail had disappeared during the Japanese occupation but did not ascribe a direct cause. Later, Ripley and Beehler (1985:8) quote a correspondent as noting "that during World War II rats were very common on Wake Island, and certainly were, in part, responsible for the demise of this rail." Their informant was R. R. Delarevelle (4 Apr 1979, Smithsonian Institution Archives, Record Unit 613, Box 502), who had been a pilot with Pan Am beginning in 1947, and would not have had any personal experience on Wake Island "during" the war.

Fuller (1987, 2001) attributed extinction to starving Japanese troops and does not mention rats. Spennemann (2006) erroneously attributed the extinction of the Wake Island Rail to a combination of the effects of Japanese feather poachers as well as the destruction and predation that took place during WW II. The feather poachers, however, cannot be invoked because the rail would have had no value in the plume trade and the feather poachers had left long before the Tanager Expedition arrived in 1923 when the rails were common (Olson 1996). We concur with Livezey's (2003:34) assessment that the species is now gone because of one of "the most direct and intense human exterminations suffered by an avian species during modern times." Livezey (2003:34) cites Blackman (1945) and Munro (1946) as the basis for the statement that "not a single record of a living specimen was made after the occupation of the island by poorly provisioned Japanese soldiers," but neither of those references mention anything whatever about Wake Island or its rail. Regardless, all available evidence points to humans, not rats, as having caused the extinction of the Wake Island Rail.

**EPILOGUE**

Its abundance, confiding nature, and accessibility would have made the Wake Island Rail ideal for in-depth studies of the ecology, behavior, and physiology of a small flightless rail, most species of which are now also extinct. Its apparently communal breeding behavior and prolonged postnatal care would have made it a particularly engaging subject for research. Now, some 70 years after the event, we can only lament the opportunity that was lost with its extinction.

With cats having been eliminated from the island (Rauzon et al. 2008a) and eradication of rodents planned for 2012, some semblance of the original ecology of Wake Atoll may eventually be restored. It would be tempting to suggest that some other species of rail might be introduced to Wake, as has been suggested for other locales (Olson 1999b, Lazell 2002, Steadman 2006). Yet we may question how much time Wake Atoll may have left to exist as a habitat for any terrestrial organisms. The Wake Island Rail, like the polar bear (*Ursus maritimus*), evolved during the last glacial interval and had never experienced a maximal interglacial rise in sea level such as occurred three times previously in the past 400,000 years (Olson et al. 2006). Sea level at those times was well above that of the present and Wake Atoll would have existed only as habitat for marine life. The human conservation ethic, so long in development and yet so far from effective implementation, must accommodate the reality that species have lives just as do individuals. Rapidly evolving species that have no refuge from the effects of Earth's climatic cycles and catastrophes will necessarily have shorter life spans than others.

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DENSITY ESTIMATES OF THE BLACK-FRONTED PIPING GUAN IN THE BRAZILIAN ATLANTIC RAINFOREST

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ABSTRACT.—We studied the Black-fronted Piping Guan (Pipile jacutinga), a medium-sized cracid (1.5 kg), endemic of Atlantic rainforest and considered endangered. We present density estimates of Black-fronted Piping Guans derived from line-transect surveys (total effort = 2,246 km) across 11 protected areas (6 continuous mainland areas, 3 non-connected mainland areas, and 2 inshore islands) in São Paulo State, southeastern Brazil. Both islands and the continuous mainland forests of Paranapiacaba massif had the highest density estimates of the species. The largest continuous mainland Atlantic Forest (Serra do Mar massif) had the lowest density estimates and the species was absent in some regions of this mountain range. All non-connected mainland forests also had low density estimates or absence of the species. Our data indicate the Black-fronted Piping Guan is not extremely sensitive to habitat disturbance and the major threat to its conservation is most likely from illegal hunting. The absence or low density estimates of the species in three survey sites is of special concern, because it is known guans are important in seed dispersal, which may have long-term consequences for forest regeneration. Received 3 September 2010. Accepted 5 April 2011.

The Atlantic coastal rainforest of South America represents the world’s most critically endangered biodiversity hotspot (Myers et al. 2000, Mittermeier et al. 2005) as only ~12.9% (194,524 km²) of the original 1.1 million km² of forest cover remains (Tabarelli et al. 2010). Much of this habitat is highly fragmented and severely impacted by deforestation through illegal logging, expansion and consolidation of agricultural landscapes, and expansion of urban areas (Dean 1996, Oliveira-Filho and Fontes 2008). More than 80% of the remnant forest fragments are estimated to be <50 ha in size and relatively isolated (Ribeiro et al. 2009). The protected areas network throughout this hotspot covers <9% of the remaining Atlantic rainforest habitat (Ribeiro et al. 2009). There are concerns the few remnant areas of Atlantic rainforest are not sufficiently extensive or of suitable ecological integrity to maintain viable populations of endemic large-bodied vertebrate species, including large-bodied birds (Marsden et al. 2005). The plight of these species is exacerbated by illegal hunting which is widespread, particularly close to more developed areas (Dean 1996, Chiarello 2000, Cullen et al. 2000, Pinto et al. 2008).

Local extinction of large-bodied frugivorous species is of special conservation concern because they may be fundamental in promoting long-distance dispersal of seeds of many endemic plant species (Théry et al. 1992, Galetti et al. 1997, Holbrook and Loiselle 2009). Few quantitative data are available on abundance and biomass of large-bodied birds in Atlantic rainforest remnants, particularly cracids, which represent some of the most important game bird species throughout Latin America and contribute most to avian biomass harvested by hunters (e.g., Silva and Strahl 1991, Thiollay 1994). Previous studies have almost exclusively focused on Amazonian cracids (e.g., Silva and Strahl 1991, Begazo and Bodmer 1998, Haugaasen and Peres 2008), whereas published data on the population abundance or density of cracids in the Atlantic rainforest biome is only available for three species: Penelope obscura, P. superciliaris (Cullen et al. 2000), and Pipile jacutinga (Galetti et al. 1997, Guix et al. 1997, Sánchez-Alonso et al. 2002, Rubim and Lemos 2008).

The Black-fronted Piping Guan (P. jacutinga) is a medium-sized cracid (1.5 kg), endemic to the Atlantic rainforest hotspot of southeastern and southern Brazil (Bahia to Rio Grande do Sul), Paraguay, and northern Argentina (Collar et al. 1992). The species is currently listed as

endangered due to ongoing and unsustainable hunting pressure, and severe habitat loss (Sick 1997, IUCN 2010). This species was formerly abundant (Sick 1997) and now has been extirpated from most of its original distribution, particularly in the Brazilian states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro (Collar et al. 1992, Galetti et al. 1997, Bernardo and Clay 2006). Currently, 33 different populations are estimated to be extant in the wild (Fig. 1) with 26 in Brazil (ICMBio 2008), four in Paraguay (Clay 2001), and three in Argentina (Benstead and Hearn 1994). A recent study in Misiones (Argentina) provided new records for the species in at least 13 localities of this region (Cockle and Bodrati 2011). The species has been successfully reintroduced in three protected areas in the Brazilian states of Minas Gerais (Ipatinga), Rio de Janeiro (Guaíraçu), and São Paulo (Paraiaba) using captive-bred individuals from the Crax Brasil breeding center in Minas Gerais and from CESP in São Paulo (ICMBio 2008).

Our objective is to present density estimates derived from data collected during a series of intensive population surveys across 11 protected areas in São Paulo State, southeastern Brazil, between 2001 and 2007. We expected to find higher density estimates of Black-fronted Piping Guans among continuous mainland forests than within the non-connected mainland and inshore islands’ remnant Atlantic rainforests because continuous mainland forests generally present higher immigration rates and, consequently, higher re-colonization rates than non-connected forests or islands (Hanski 1999).
### TABLE 1. Characteristics of study sites in Atlantic rainforest remnants of São Paulo State, Brazil.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Size (ha)</th>
<th>Park creation (year)</th>
<th>Connectivity</th>
<th>Altitudinal range (m)</th>
<th>Study period</th>
<th>Number of park rangers</th>
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<td>Island</td>
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<td>Continuous</td>
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<td>2004-2006</td>
<td>12</td>
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<td>2005-2006</td>
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<td>500-1,298</td>
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<td>Parque Estadual Serra do Mar – Cunha (Cun)</td>
<td>11,660</td>
<td>1974</td>
<td>Continuous</td>
<td>1,100-1,820</td>
<td>2002-2003</td>
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</table>

* According to IF (2011) and park managers.

### METHODS

**Study Areas.**—We surveyed nine large areas ranging from 111 to 1,500 km² of mainland remnant Atlantic rainforest (6 continuous and 3 non-connected forests), and two forested inshore islands in São Paulo State, Brazil (Table 1). These legally protected areas comprise some of the few largest Atlantic rainforest remnants, including the Serra do Mar and Serra de Paranapiacaba mountain ranges (Table 1). The inshore island of Ilha do Cardoso is a land-bridge island and its closest point to the continent is 300 m. The oceanic inshore island of Ilhabela is 1.7 km from the nearest point of the continent. All areas were dominated by three different types of forest habitat, which vary according to the latitude and altitude: lowland rainforest, and submontane and lower montane rainforest (Oliveira-Filho and Fontes 2000). Mean annual temperatures of these areas vary between 17 and 25°C (IF 2011).

All study areas have experienced palm-heart (Euterpe edulis) harvesting and illegal hunting (Galetti and Fernandez 1998, Aguiar et al. 2003, Olmos et al. 2004, Galetti et al. 2009). All areas are part of two Endemic Bird Areas (BirdLife International 2003): Atlantic Forest lowlands and Atlantic Forest mountains. They are also considered Important Bird Areas (IBA), except Ilha do Cardoso and Jurupurá (Statteersfield et al. 1998).

**Bird Surveys.**—We used a variable-distance line-transect method (e.g., Buckland et al. 1993) to survey populations of Black-fronted Piping Guans following standardized methodology derived by Peres (1999) and used by Galetti et al. (2009). Between three and 14 transects were systematically positioned at each site to be representative of the surrounding habitat (Peres 1999). Transect locations were selected mainly by vegetation type, elevation and distance from rivers and roads, and the variation in these habitat features were well represented in our study areas. Transect length varied from 0.7 to 8.4 km, depending upon local topography and forest patch size (Galetti et al. 2009) (Table 2). Ten observers, who were fully trained in distance sampling techniques and cracid identification, were responsible for conducting the bird surveys at all sites during 2001 to 2007. Transects were surveyed systematically during 0615 and 1730 hrs by one or two observers, once a month at each site, with direction of travel along each transect rotated between subsequent surveys to minimize the effect of time of day. We recorded the date, time, global positioning system (GPS) co-ordinates, number of individuals seen and perpendicular distance to the line transect (accurately obtained with a measuring tape) for each piping guan detected. Survey effort at each site ranged from 103.1 to 273 km (Table 2), which is greater than the sampling effort required for reliable abundance estimates of large birds (Thoisy et al. 2008).
TABLE 2. Total effort (km), number of encounters, relative abundance (encounters/10 km) and mean density as individuals/km² and groups/km² (95% confidence interval) of Black-fronted Piping Guans in 11 Atlantic rainforest remnants in São Paulo State, Brazil (study areas correspond to Table 1).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Total number of transects</th>
<th>Length of transects (m)</th>
<th>Total km walked</th>
<th>Number of encounters</th>
<th>Relative abundance (encounters/10 km)</th>
<th>Density (Range) (individual/km²)</th>
<th>Density (Range) (groups/km²)</th>
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<tr>
<td>Islands</td>
<td></td>
<td></td>
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<tr>
<td>PEIC</td>
<td>14</td>
<td>700-4,000</td>
<td>273</td>
<td>10</td>
<td>0.4</td>
<td>3 (2.4–3.5)</td>
<td>2 (1.6–2.3)</td>
</tr>
<tr>
<td>PEI</td>
<td>11</td>
<td>900-5,500</td>
<td>188</td>
<td>29</td>
<td>1.5</td>
<td>13.3 (11–16.2)</td>
<td>8 (6.7–9.8)</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>PECB</td>
<td>9</td>
<td>1,200–5,400</td>
<td>237</td>
<td>17</td>
<td>0.7</td>
<td>4.4 (3.6–5.3)</td>
<td>3.7 (3.1–4.5)</td>
</tr>
<tr>
<td>PETAR</td>
<td>7</td>
<td>1,400–8,000</td>
<td>256</td>
<td>10</td>
<td>0.4</td>
<td>3 (2.5–3.7)</td>
<td>2 (1.7–2.5)</td>
</tr>
<tr>
<td>PEJa</td>
<td>5</td>
<td>700–4,500</td>
<td>103</td>
<td>1</td>
<td>0.1</td>
<td>0.5 (0.4–0.6)</td>
<td>0.5 (0.4–0.6)</td>
</tr>
<tr>
<td>PEJu</td>
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<td>1,500–4,500</td>
<td>222</td>
<td>0</td>
<td>Not found</td>
<td>Not found</td>
<td>Not found</td>
</tr>
<tr>
<td>Serra do Mar Massif</td>
<td></td>
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<td></td>
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<tr>
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<td>700–3,350</td>
<td>190</td>
<td>1</td>
<td>0.1</td>
<td>0.27 (0.23–0.33)</td>
<td>0.27 (0.23–0.33)</td>
</tr>
<tr>
<td>Car</td>
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<td>700–3,000</td>
<td>138</td>
<td>1</td>
<td>0.1</td>
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<td>0.4 (0.3–0.5)</td>
</tr>
<tr>
<td>Cun</td>
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<td>1,050–8,450</td>
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<tr>
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<tr>
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<td>210</td>
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<td>Not found</td>
<td>Not found</td>
</tr>
</tbody>
</table>

Data Analyses.—Distance data were analyzed using Program DISTANCE Version 5.1 (Thomas et al. 2006). Key function selection was evaluated using Akaike’s Information Criteria (AIC) and a Chi-square statistic was used to assess the ‘goodness of fit’ of each function (Buckland et al. 1993, 2001). Repeated line transects increased sample sizes at each site, providing more precise estimates of variance and increasing the reliability of the detection function (Buckland et al. 2001, Lee and Marsden 2008). We had small sample sizes (between 1 and 29 encounters in each area, Table 2), and used a generalized effective strip width (ESW = 9.6 m, 95% confidence interval = 7.9–11.7 m) obtained by pooling all observation data of Black-fronted Piping Guans. Pooling all records generated a more precise modeling of piping guan detection because the combined AIC values of the separate forest site detection functions were greater than the AIC value for the pooled detection function (Buckland et al. 2001, Lee and Marsden 2008). This procedure allowed us to calculate a single detection curve (half-normal key distribution with cosine adjustments) and provided a more reliable estimate of species density (individuals/km²) (Buckland et al. 1993). Encounter rates (number of encounters/10-km transect) were calculated for all sites as an estimate of relative abundance.

RESULTS

We recorded 70 observations of Black-fronted Piping Guans across the 11 study sites from 2001 to 2007 during 2,246 km of line transects. All individuals were recorded in trees at heights between 5 to 10 m and, as rare events, some birds were observed 20 m above the ground, frequently on isolated heart-of-palm trees (Euterpe edulis). The birds were recorded close to each transect (95% confidence limits = 7.9–11.7 m), as shown by the effective strip width value (mean = 9.6 m, CV = 10%). Detection probability decreased with increasing distance (Fig. 2), mainly because the dense understory and abundant vines made observations of the species difficult at longer distances.

Most birds observed were either solitary (60% of all records) or in pairs (33% of all records) and were only observed in larger groups (range = 3–5 individuals) in 7% of the occasions. Pairs were seen <5 m from each other over all years. The majority of visual records (51%) occurred during the morning (28% of the records between 0900 and 1200 hrs and 23% between 0800 and 1000 hrs).

The number of observations recorded and density estimates varied among sites (Table 2). The low overall mean density estimate (1.6 individuals/km², range = 1.2–2.2 individuals/km²) demonstrated how difficult it was to record the species in the largest Brazilian Atlantic Forest remnants. At least four populations were found in São Paulo State: two in the inshore islands, a small population in Serra do Mar massif, and a larger one in Serra de Paranapiacaba massif.
Perpendicular distance (m)

FIG. 2. Detection probability of Black-fronted Piping Guans as a function of the distance to the observer. The columns represent the number of detections in different distance classes, and the line represents the fit detection function (Software DISTANCE 5.1).

(Fig. 3). We considered a population as a set of individuals living in the same region which had no interaction with other individuals living in other regions.

The inshore islands and the contiguous protected areas of Paranapiacaba massif had the highest density estimates (DE) of this species (>10 observations and >2 groups/km². Table 2). The highest number of observations and DE were recorded from Ilhabela Island (29 encounters or 41% of the records, DE = 8 groups/km². Table 2).

FIG. 3. Density estimates of Black-fronted Piping Guans in protected areas of São Paulo State (1 = Jurupará, 2 = Carlos Botelho, 3 = PETAR, 4 = Jacupiranga, 5 = Ilha do Cardoso, 6 = Juréia-Itatins, 7 = Ilhabela, 8 = Caraguatatuba, 9 = Santa Virgínia/Cunha, 10 = Picinguaba, 11 = Pilões).
The largest continuous mainland Atlantic Forest (Serra do Mar massif) had a low density; a similar pattern was found for the non-connected mainland forests (DE <0.5 groups/km\(^2\)) with no observations in two continuous forests and one non-connected area (Table 2).

**DISCUSSION**

We added to the knowledge of the global population status of Black-fronted Piping Guans, as we studied ~36% of the currently known world occurrence sites of this species. Line-transect methodology was adequate for our surveys, and we highly recommend use of this method for other areas where the species is present, mainly in southern Brazil and Paraguay. However, this methodology requires great effort considering the total number of km walked (2,241 km walked) and low number of observations (70). Pooling all observations in areas with few observations per study area was needed to obtain an effective strip width estimate. This allowed more precise density estimates based on >40 sightings, as recommended by Buckland et al. (2001).

The probability detection from the transect line up to 4.6 m was 100% (Fig. 2) indicating observers detected all birds on the transect line which met an important assumption of the method. Probability of detection decreased with increasing distance, as expected, because the dense understory and canopy made bird detection difficult. The probability of detection was ~50% and was between 4.7 and 13 m. Black-fronted Piping Guans have discrete movements and calls, and it is likely that some individuals were not detected at distances >4.7 m. Thus, our estimates should be considered conservative.

The differences in density values among areas are suggestive and not conclusive because we had insufficient sample sizes for statistical analysis. We had high density estimates in continuous forests of the Paranapiacaba massif and inshore islands. These densities were higher than in the continuous forests of the Serra do Mar massif, which is the largest remnant Atlantic rainforest.

Density estimates of Black-fronted Piping Guans in the Serra do Mar massif were the lowest obtained in our study (<0.5 individuals/km\(^2\)) and far below the average density estimates for other cracids in the Amazon and Andes regions (e.g., Silva and Strahl 1991, Thiollay 1994, Rios et al. 2005, Londono et al. 2007, Hill et al. 2008, Setina 2009). Densities in the Serra do Mar were higher than those obtained for other cracids in only two areas of the Amazon forest: Razor-billed Curassow (*Mitu tuberosum*) in an area of high hunting pressure (0.02 individuals/km\(^2\)) and Spix’s Guan (*Penelope jacquacu*) in an area of low hunting pressure (0.19 individuals/km\(^2\)) (Begazo and Bodmer 1998, Haugaasen and Peres 2008). The conservation status of Black-fronted Piping Guans in the Serra do Mar region is of concern because local extinction can occur when population densities are low. This is a priority area for conducting more research and conservation action, e.g., population supplementation, if threats are eliminated.

Sánchez-Alonso et al. (2002) surveyed the Paranapiacaba area in 1998 (Intervales, Carlos Botelho, and Alto Ribeira parks), using the line-transect method, and estimated a mean density of 2.67 birds/km\(^2\). Our mean density estimates in Paranapiacaba massif are between 3.0 and 4.4 individuals/km\(^2\) (Table 2) and suggest Carlos Botelho is an important area for Black-fronted Piping Guan conservation. Immigration of the species from Paranapiacaba to surrounding patches may occur, e.g., Parque do Zizo (adjacent to Carlos Botelho), that apparently also have populations (C. O. Gussoni, pers. comm.).

Galetti et al. (1997) presented density estimates of Black-fronted Piping Guans in several areas of Atlantic rainforest, but our data are not comparable due to differences in methodologies. We recorded more observations in Ilhabela and Ilha do Cardoso, but lower numbers per group. The Black-fronted Piping Guan only flies short distances and the closest distance from Ilhabela to the mainland is >1 km; thus, we believe this population is isolated although the species can cross the narrow (~300 m) channel between Ilha do Cardoso and the mainland. Galetti et al. (1997) indicated the population of Black-fronted Piping Guans on Ilha do Cardoso had been extirpated based on no records between 1994 and 1995. Our study demonstrated the species is present in Ilha do Cardoso and the population density is higher than in some larger mainland regions. The absence of the Black-fronted Piping Guan records in Jurupará Park suggests movements among forests of Paranapiacaba and Serra do Mar may no longer occur (Fig. 3).
CONSERVATION IMPLICATIONS

Some observations occurred near highways with heavy traffic (Jacupiranga and Santa Virginia parks), altered forest (bamboo forest in Ilhabela Park) and areas dominated by Cecropia spp. (Ilha do Cardoso Park). Galetti et al. (1997) also reported Black-fronted Piping Guans in young forests dominated by Cecropia spp. (Jureia Park), and in monoculture of Pinus (Carlos Botelho Park). These observations occurred in areas surrounded by mature forest, but our data indicate Black-fronted Piping Guans are not extremely sensitive to habitat disturbance and the major threat to its conservation is most likely from illegal hunting. Cracids can be used as indicators of hunting pressure (Strahl and Grajal 1991, Strahl and Silva 1997) and studies demonstrating hunting pressure in all areas with Black-fronted Piping Guans can be done similarly to those of Silva and Strahl (1991), Begazo and Bodmer (1998), and Peres (2000).

All protected areas of São Paulo State studied have human occupation and are understaffed (according to park managers, a single park ranger is usually responsible for patrolling >1,700 ha). These areas have illegal activities including hunting, palm-heart extraction, and logging (Galetti and Fernandez 1998, Galetti et al. 2009). An obvious recommendation is to increase the number of park rangers in all areas, as well as effective law enforcement. Easy access to protected areas also increases hunting pressure (Peres and Terborghi 1995, Galetti et al. 2009). In addition to evidence of hunting, we also observed domestic dogs (Canis lupus familiaris) in all areas surveyed and it is well known they can impact bird biodiversity (Galetti and Sazima 2006, Bernardo 2010).

The absence or low density estimates of the species in three survey sites is of special concern, because it is known that guans are important in seed dispersal (Galetti et al. 1997, Sedaghatkshi et al. 1999). This species eat fruits ranging from tiny drupes (0.4 mm diam) to large (25 mm diam) arilate seeds (Galetti et al. 1997). Thus, the absence of Black-fronted Piping Guans may have consequences for long-term forest regeneration.

ACKNOWLEDGMENTS

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LITERATURE CITED


CLAY, R. P. 2001. The status and conservation of cracids in...


BLACK-FRONTED PIPING GUAN DENSITY ESTIMATES
EFFECTS OF STOP-LEVEL HABITAT CHANGE ON CERULEAN 
WARBLER DETECTIONS ALONG BREEDING BIRD SURVEY ROUTES 
IN THE CENTRAL APPALACHIANS 

PATRICK M. McELHONE, PETRA BOHALL WOOD, AND DEANNA K. DAWSON

ABSTRACT.—We examined the effects of habitat change on Cerulean Warbler (Dendroica cerulea) populations at stops along Breeding Bird Survey (BBS) routes in the central Appalachians. We used aerial photographs to compare early (1967/1971), middle (1982/1985), and late (2000/2003) periods and compared 1992 and 2001 National Land Cover Data (NLCD). Mean Cerulean Warbler detections per stop decreased at 68 BBS stops between the early (0.05) and middle (0.01) time periods and their distribution became more restricted (15 vs. 3% of stops), but the amount of deciduous/mixed forest increased. Mean detections at 240 stops decreased from the middle (0.09) to the late (0.06) time periods, but the deciduous/mixed forest land cover and fragmentation metrics did not change. The amounts of deciduous/mixed forest, core forest area, and edge density in the NLCD analysis decreased from 1992 to 2001, whereas the amount of non-forest land cover increased. The number of Cerulean Warbler detections did not change (1992 = 0.08, 2001 = 0.10; \(P = 0.11\)). The lack of concordance between Cerulean Warbler detections and broad habitat features suggests that smaller, microhabitat features may be most important in affecting Cerulean Warbler breeding habitat suitability.

Received 10 October 2009. Accepted 31 March 2011.

The Cerulean Warbler (Dendroica cerulea) is considered a species of high conservation concern by Partners in Flight and has been reviewed for listing as a threatened species (USDI 2006). Analyses of data from the North American Breeding Bird Survey (BBS) indicated Cerulean Warbler populations declined range-wide at 4.1% per year during 1966–2007 (Sauer et al. 2008). The consistent decline of Cerulean Warblers in the core breeding range over the 40 years of the BBS elevated this species to a high level of conservation concern, and led to creation of the Cerulean Warbler Technical Group (Hamel et al. 2004).

The Ohio Hills and Cumberland Plateau physiographic areas of the Appalachian Mountain Bird Conservation Region (BCR 28; http://www.nabci-us.org/map.html) are the core breeding range for Cerulean Warblers (Hamel 2000b, Sauer et al. 2008). Mesic upland forests, particularly ridgetops, are important habitat within the core range (Rosenberg et al. 2000, Weakland and Wood 2005). Cerulean Warblers require large tracts of mature forests with tall deciduous trees to sustain viable breeding populations (Oliarnyk 1996, Hamel 2000a).

Habitat loss and fragmentation from land use changes are thought to be major factors contributing to declining populations in the core breeding range (Hamel et al. 2004, Buehler et al. 2008). Donovan and Flather (2002) identified the effects of land use changes on Cerulean Warbler populations in the Appalachian Region as high priority for research. Recent research has begun to assess the effects of large-scale habitat change and fragmentation on Cerulean Warbler populations in the region (Weakland and Wood 2005; Wood et al. 2005, 2006). Analysis of the relationship of changes in Cerulean Warbler counts to habitats along BBS routes in the core breeding range may provide insight into the role habitat change has in long-term population declines.

The BBS, established in 1966 to monitor breeding bird populations, is the primary data source for population status of landbirds across North America (O’Connor et al. 2000). Each 40-km BBS route consists of 50 point-count stops, 0.8 km apart along secondary roads. Routes are surveyed once each year by volunteer observers, who identify and count all birds seen within 400 m or heard within a 3-min period at each stop (Robbins et al. 1986). Routes are distributed randomly and are assumed to reflect representative habitats (Donovan and Flather 2002). BBS counts used in analysis of population trends are
summed across all 50 stops; they represent a composite of the habitats encountered and stop-specific changes in habitat are overshadowed (Sauer 1999). A more in-depth approach to examine how habitat changes affect Cerulean Warbler population trends on BBS routes is to analyze data at each stop instead of across the entire route. Small scale habitat characteristics, including slope position, aspect, and microhabitat features such as canopy gaps, can affect Cerulean Warbler abundance (Weakland and Wood 2005, Perkins 2006); these features are lost when habitat is analyzed at the route level.

We examined the association between change in the Cerulean Warbler population and habitat at stops along BBS routes in the core breeding range. We (1) analyzed the effects of land cover and forest fragmentation changes, measured from aerial photographs, on Cerulean Warbler populations over three time periods at stops on a subsample of BBS routes to examine long-term changes; and (2) quantified land cover and forest fragmentation metrics at BBS stops over two time periods using National Land Cover Data (NLCD) to examine effects of more recent habitat changes on Cerulean Warbler populations along a broader sample of BBS routes.

**METHODS**

**Study Area.**—We used survey data from BBS routes within the West Virginia, Kentucky, and Ohio portions of BCR 28 (Fig. 1). The study area is within NLCD mapping zones 47, 53, 61, and 62 (Homer et al. 2004). The Ohio Hills, Northern Cumberland Plateau, and Mid Atlantic Ridge and Valley physiographic regions (www.partnersinflight.org/bcplans/piplans.htm) of BCR 28 comprise most of the study area. The Ohio Hills (~8 million ha) is characterized by dissected plateaus ranging from 150 to 450 m in elevation (Rosenberg 2000). The Northern Cumberland Plateau (~5.5 million ha) is a rolling hills tableland ranging from 300 to 580 m in elevation (Dearest 2003). The Mid Atlantic Ridge and Valley (~5 million ha) is dominated by long mountainous ridges and intervening valleys ranging from 100 to 1,100 m in elevation (Rosenberg 1999). Dominant land cover of each physiographic area is mixed mesophytic forests consisting primarily of oaks (*Quercus* spp.) and hickories (*Carya* spp.).

**Data Collection.**—We used data from BBS routes within the study area that met three criteria. (1) Selected routes had at least one stop with detections of Cerulean Warblers within at least one time period. Our study examined how change in land cover and habitat may have affected detections of Cerulean Warblers, and routes that did not have a single detection lacked this information. (2) We included only BBS routes with stop-level Global Positioning System (GPS) coordinates collected in recent years by route observers so stops could be mapped as accurately as possible. Route observers at times adjust stop locations to safer or quieter stopping points; stop locations mapped by third parties may not be accurate. Stops were not included if the route path was changed between time periods. (3) We only used BBS routes that were surveyed at least three times within the 5 years centered on each year of available land cover data. Survey data over multiple years better identify stops at which Cerulean Warblers actually were present but were missed in some years. Birds can be missed in a 3-min counting period and, if not detected, cannot be assumed to be absent. The 3–5 year period also may provide a more accurate measure of the response of Cerulean Warblers to habitat changes than data from only 1 year, which would be more of a snapshot in time. Using BBS data from years that bracket the land cover data ensured that land cover was representative of conditions when the routes were surveyed.

Land cover data can be measured from several remotely-sensed data sources; we used aerial photographs and the NLCD in our study. Aerial photographs have been taken occasionally within the study area over the lifetime of the BBS and are most suited to investigate long-term changes in land cover along BBS routes. However, aerial photographs are spatially limited, do not provide complete coverage of many BBS routes, and hand-digitizing land cover from them is time-consuming. The NLCD allows land cover to be quickly assessed for a broader extent of BBS routes. However, aerial photographs are spatially limited, do not provide complete coverage of many BBS routes, and hand-digitizing land cover from them is time-consuming. The NLCD allows land cover to be quickly assessed for a broader extent of BBS routes, but was limited to 1992 and 2001 at the time of our study. Thus, we used aerial photographs to examine long-term land cover changes at a subset of BBS stops and NLCD data to quantify changes in land cover over a shorter time period for BBS stops along 28 routes.

Aerial photograph data were separated into three periods: 1967/1971 (early), 1982/1985 (middle), and 2000/2003 (late) to correspond with years that aerial photographs were available. We used aerial photographs taken during leaf-off (Oct to early May) when it is possible to distinguish
coniferous from deciduous trees. Six of the 88 BBS routes in the study area (5 routes in West Virginia, 1 in Ohio) had aerial photographs available for appropriate years and met our three criteria for inclusion. Aerial photographs were available for 240 stops on all six routes for the middle to late time period but for only 68 stops on two routes for the early to middle time period (Table 1). Photographs from all time periods were rectified and digitized in ArcMap, Version 9.2 (ESRI, Redlands, CA, USA). Aerial photographs from different years or sources had different resolutions, and we digitized land cover at the minimum scale available (1:60,000). We digitized land cover into four types: a combined deciduous/mixed forest type, coniferous forest, developed, and agriculture. We distinguished between deciduous/mixed and coniferous forests because Cerulean Warblers are not known to use coniferous forests (Hamel 2000a). The agriculture land cover collapsed all remaining types not included by the three other land cover types and was dominated by agricultural land.

Twenty-eight BBS routes with 1,375 stops (Table 1) met criteria to be included for comparison of the 1992 and 2001 NLCD data. Development is an important land cover class that is changing over time along BBS routes, but we were not able to use this class for the NLCD data sets. Small, secondary roads were not classified in the 1992 NLCD, but in 2001 they were classified as the developed type (Vogelmann et al. 2001, Homer et al. 2004). Thus, differences in developed area around a BBS stop could be the result of different classification methods rather than a change in land cover; thus, we combined
TABLE 1. BBS routes used in aerial photograph and NLCD analyses. Aerial photographs were compared between the early (1967/1971) and middle (1982) time periods, and between the middle (1982/1985) and late (2000/2003) time periods.

<table>
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<td>X</td>
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<td>X</td>
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<td></td>
<td>X</td>
</tr>
<tr>
<td>84066901</td>
<td>OH</td>
<td>Wayne National Forest</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84066903</td>
<td>OH</td>
<td>Zaleski State Forest</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84066904</td>
<td>OH</td>
<td>Tar Hollow</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090005</td>
<td>WV</td>
<td>Bramwell</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090014</td>
<td>WV</td>
<td>Spencer</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090016</td>
<td>WV</td>
<td>Nicut</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090022</td>
<td>WV</td>
<td>Canaan</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090024</td>
<td>WV</td>
<td>Three Forks</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090026</td>
<td>WV</td>
<td>Cedarville</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090028</td>
<td>WV</td>
<td>Strange Creek</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090037</td>
<td>WV</td>
<td>Moundsville</td>
<td></td>
<td>X</td>
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<tr>
<td>84090038</td>
<td>WV</td>
<td>Monongah</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090039</td>
<td>WV</td>
<td>McDonald</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090041</td>
<td>WV</td>
<td>Beebe</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090044</td>
<td>WV</td>
<td>Greer</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090051</td>
<td>WV</td>
<td>Martinsburg</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090052</td>
<td>WV</td>
<td>Clinton</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090053</td>
<td>WV</td>
<td>RuthBelle</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>84090147</td>
<td>WV</td>
<td>Bismark</td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

Land cover was quantified within a 300-m buffer around each stop from aerial photographs and the NLCD. Cerulean Warblers rarely are detected beyond 100 m on point counts (Bosworth 2003) and their territories average 0.3–1.0 ha in size (Ollarnyk and Robertson 1996, Barg et al. 2005, Perkins 2006); thus, the 300-m (28.3 ha) buffer is sufficiently large to accommodate territories of several Cerulean Warblers. We calculated area of each land cover polygon, and summed area for each land cover type per BBS stop. The NLCD was reclassified to the three land cover types and the area was tabulated for each type around each stop. We used the percentage of each land cover type for analyses because the raster grid cells of the NLCD do not create a perfect circle around each of the route stops and, as a result, the total area around each buffered stop was ~28.3 ha.

We also calculated change over time in several forest fragmentation metrics for the aerial photograph and NLCD data sets. Cerulean Warblers prefer large tracts of unfragmented deciduous forests (Hamel 2000a, Weakland and Wood 2005), and we included maximum size of deciduous/mixed forest patch (ha), core area of deciduous/mixed forest (%), and edge density (m/ha). Maximum size forest patch was the size of the largest deciduous/mixed forest polygon within the 300-m buffer around the stop. Core forest area was the amount of deciduous/mixed forest >60 m from an edge converted to percentage of core forest in each buffer. Edge effects are known to occur within 50 m of a forest edge (Paton 1994) and other studies have used 50 m in analyses (Hazler et al. 2006, Wood et al. 2006). Edge...
density was the amount of linear edge relative to the total land area at each buffered stop (McGarigal et al. 2002). We used the four land cover classes for the aerial photograph data set and weighted a coniferous forest edge as zero and a developed or agriculture edge as one. Forest-nonforest edge density for the NLCD data set was the amount of linear edge between deciduous/mixed forest and non-forest patches; forest-forest edge density was the amount of linear edge created by a road splitting deciduous/mixed forest patches. We calculated forest-nonforest edge density because Cerulean Warblers may use gaps in forest created by roads (Weakland and Wood 2005, Perkins 2006). Roads were not included in the 1992 NLCD classification scheme (Vogelmann et al. 2001, Homer et al. 2004) and the 30-m cell size of the NLCD may not account for smaller roads in the 1992 and 2001 NLCD. Thus, we incorporated a general roads layer into both NLCD data sets, including roads as small as jeep trails from the U.S. Detailed Streets data set (http://www.esri.com/metadatal76iiprof80.dtl) following McElhonne (2009).

Count data for Cerulean Warblers at stops along the selected BBS routes were obtained from BBS staff (USGS, Patuxent Wildlife Research Center, Laurel, MD, USA). Stop-level count data after 1996 were downloaded from www.pwrc.usgs.gov/bbsapps/index.cfm. We extracted earlier data from the BBS field sheets. Cerulean Warbler detections were averaged within the 3-5 year time bracket surrounding each aerial photograph or NLCD year.

Statistical Analyses.—Statistical analyses were conducted using SAS (SAS Institute Inc. 2004) with \( \alpha = 0.10 \). Univariate analyses indicated variables were not normally distributed, and we transformed them using the most appropriate method to achieve normality. We used arcsine square root transformation on percent of each land cover type and percent forest core area, and a logarithmic transformation for maximum forest patch, edge density, forest-forest edge density, and forest-nonforest edge density. A square root transformation was applied to average and maximum Cerulean Warbler counts because of their poisson distribution (Zar 1996).

We examined long-term changes in habitat over the entire BBS survey period by comparing the four land cover classes (deciduous/mixed forest, coniferous forest, developed, agriculture) and three fragmentation metrics (max size forest patch, forest core area, edge density) between the early and middle time periods (68 stops on 2 routes) and between the middle and late time periods (240 stops on 6 routes) with ANOVA (Ritchie et al. 1998). Each ANOVA model included route, period, and stop within route. We compared Cerulean Warbler detections between the early and middle time periods, and between the middle and late time periods using ANCOVA (Welsh and Ollivier 1998) with variables: route, period, and stop within route. Covariates were percentage of each land cover in each time period. Stop within route was the error term in the ANOVA and ANCOVA models for testing differences between time periods. We repeated comparisons between the middle and late time periods using only stops that had a Cerulean Warbler detected during at least one period (i.e., a presence-only analysis).

We examined recent habitat changes by comparing three land cover classes (deciduous/mixed forest, coniferous forest, non-forest) and four fragmentation metrics (max size forest patch, core forest, forest-forest edge density, forest-nonforest edge density) between 1992 and 2001, and NLCD data for 1,375 stops on 28 BBS routes with ANOVA. We also compared land cover and fragmentation metrics between the 1992 and 2001 NLCD data, using only those stops where at least one Cerulean Warbler was detected (344 stops from 28 routes).

We compared mean and maximum Cerulean Warbler detections between time periods for all stops and for those stops at which the species was detected using ANCOVA with the variables: route, period, and stop within route. Covariates were percentage of each land cover in each time period. The analysis of all stops along a route allowed us to examine habitat changes across landscapes where Cerulean Warblers were known to occur. Analysis of stops that had at least one Cerulean Warbler detected allowed us to examine local conditions where Cerulean Warblers actually were detected.

RESULTS

Aerial Photograph Analysis for 1967/1971 vs. 1992.—Deciduous/mixed forest cover increased from the early to middle time period at 68 stops on two BBS routes (Table 2), whereas agriculture land cover decreased. The amount of coniferous forest and developed land cover did not change, and none of the fragmentation metrics...
TABLE 2. Land cover and fragmentation metrics based on aerial photographs for the early (1967/1971) and middle (1982) time periods and Cerulean Warbler detections during 5 years surrounding each aerial photograph year for 68 stops on two BBS routes in West Virginia and Ohio (df = 66).

<table>
<thead>
<tr>
<th>Category</th>
<th>Early</th>
<th>Middle</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landcover %</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous/mixed forest</td>
<td>36.3 ± 3.1</td>
<td>49.3 ± 3.40</td>
<td>3.82</td>
<td>0.06</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>1.5 ± 0.6</td>
<td>2.3 ± 1.15</td>
<td>0</td>
<td>0.98</td>
</tr>
<tr>
<td>Developed</td>
<td>16.8 ± 2.4</td>
<td>14.7 ± 2.11</td>
<td>0.32</td>
<td>0.57</td>
</tr>
<tr>
<td>Agriculture</td>
<td>45.4 ± 3.1</td>
<td>33.9 ± 3.16</td>
<td>5.30</td>
<td>0.02</td>
</tr>
<tr>
<td>Fragmentation metrics</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max forest patch (ha)</td>
<td>6.8 ± 0.6</td>
<td>8.8 ± 0.6</td>
<td>1.10</td>
<td>0.30</td>
</tr>
<tr>
<td>Core forest (%)</td>
<td>7.8 ± 1.2</td>
<td>10.6 ± 1.8</td>
<td>0.68</td>
<td>0.41</td>
</tr>
<tr>
<td>Edge density (m/ha)</td>
<td>138.6 ± 5.3</td>
<td>136.8 ± 4.6</td>
<td>0</td>
<td>0.99</td>
</tr>
<tr>
<td>Cerulean Warblers detections/stop</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.05 ± 0.02</td>
<td>0.01 ± 0.007</td>
<td>5.25</td>
<td>0.03</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.16 ± 0.05</td>
<td>0.03 ± 0.020</td>
<td>5.48</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Differed between the early and middle time periods. Average and maximum Cerulean Warbler detections per stop decreased (Table 2) and Cerulean Warblers were detected at fewer stops (15% in the early period vs. 3% in the middle period).

Aerial Photograph Analysis for 1982/1985 vs. 2000/2003.—Amount of developed land cover increased and agriculture decreased around 240 stops on six BBS routes between the middle and late time period (Table 3). Core forest increased, but other forest metrics (forest land covers, max size forest patch, and edge density) did not change (Table 3). Average number of Cerulean Warbler detections per stop decreased, but the maximum number counted did not change between these two time periods and perenni stops with detections was similar (27% stops in the middle period and 30% in the late period). Cerulean Warblers were detected at 76 of the 240 stops during either the middle (65 Cerulean Warblers detected) or late time period (71 Cerulean Warblers detected); 44 stops had detections in both time periods (18% of stops).

Developed land cover increased and agriculture land cover decreased (Table 3) from the middle to late period at 76 stops where Cerulean Warblers were detected, although both land covers were less abundant than for all stops. We found no change in deciduous/mixed or coniferous forest and none of the fragmentation metrics differed between the middle and late time periods. Average number of Cerulean Warbler detections per stop decreased more markedly than in the all stops analysis and the maximum number detected approached a significant decline (P = 0.10).

NLCD Analysis for 1992 vs. 2001.—The deciduous/mixed forest and coniferous forest land cover types decreased, whereas the non-forest type increased at 1,375 stops on 28 routes (Table 4). Forest patch size increased, whereas core forest, forest-forest edge density, and forest-nonforest edge density decreased. Cerulean Warblers were detected at 14% of stops in 1990-1994 and 17% in 1999-2003. Average and maximum Cerulean Warbler detections per stop were not different, although counts increased slightly and approached significance (P = 0.11).

Cerulean Warblers were detected at 344 of 1,375 stops in both time periods. Coniferous and deciduous/mixed forests decreased at these stops (Table 4), while non-forest land cover increased from 15 to 25%. Maximum size of forest patch and forest-nonforest edge density increased, forest-forest edge density decreased, and amount of core forest did not change. The mean and maximum number of Cerulean Warblers detected increased.

DISCUSSION

Historic Habitat and Cerulean Warbler Changes: 1967/1971 vs. 1982.—Several land covers changed at 68 stops along the two BBS routes for which we analyzed aerial photographs from the early to middle time periods. The increase in deciduous/mixed forest and decline in agriculture land cover...
TABLE 3. Land cover and fragmentation metrics based on aerial photographs for the middle (1982/1985) and late (2000/2003) time periods and Cerulean Warbler detections during 5 years surrounding each aerial photograph year for all 240 stops (df = 234) and 76 (df = 70) presence-only stops on six BBS routes in West Virginia and Ohio.

<table>
<thead>
<tr>
<th>Landcover (%)</th>
<th>Middle</th>
<th>Late</th>
<th>F</th>
<th>P</th>
<th>Middle</th>
<th>Late</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous/mixed forest</td>
<td>58.9 ± 1.7</td>
<td>62.0 ± 1.6</td>
<td>0.97</td>
<td>0.32</td>
<td>69.9 ± 2.5</td>
<td>74.4 ± 2.1</td>
<td>0.73</td>
<td>0.39</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>1.0 ± 0.4</td>
<td>0.8 ± 0.3</td>
<td>0.16</td>
<td>0.69</td>
<td>1.1 ± 0.6</td>
<td>0.7 ± 0.6</td>
<td>0.92</td>
<td>0.34</td>
</tr>
<tr>
<td>Developed</td>
<td>9.7 ± 1.0</td>
<td>14.7 ± 1.4</td>
<td>9.4</td>
<td>0.002</td>
<td>5.4 ± 1.2</td>
<td>8.6 ± 1.4</td>
<td>5.08</td>
<td>0.03</td>
</tr>
<tr>
<td>Agriculture</td>
<td>30.5 ± 1.6</td>
<td>22.5 ± 1.4</td>
<td>9.88</td>
<td>0.002</td>
<td>23.7 ± 2.2</td>
<td>16.3 ± 1.8</td>
<td>4.28</td>
<td>0.04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fragmentation metrics</th>
<th>Middle</th>
<th>Late</th>
<th>F</th>
<th>P</th>
<th>Middle</th>
<th>Late</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max forest patch (ha)</td>
<td>13.4 ± 0.3</td>
<td>10.4 ± 0.3</td>
<td>2.5</td>
<td>0.12</td>
<td>11.2 ± 0.1</td>
<td>12.0 ± 0.5</td>
<td>1.33</td>
<td>0.25</td>
</tr>
<tr>
<td>Core forest (%)</td>
<td>14.8 ± 0.9</td>
<td>16.6 ± 0.8</td>
<td>2.96</td>
<td>0.09</td>
<td>18.9 ± 1.4</td>
<td>20.9 ± 1.3</td>
<td>0.92</td>
<td>0.34</td>
</tr>
<tr>
<td>Edge density (m/ha)</td>
<td>142.1 ± 3.0</td>
<td>144.8 ± 3.3</td>
<td>0.08</td>
<td>0.77</td>
<td>139.9 ± 5.6</td>
<td>139.3 ± 6.1</td>
<td>0.04</td>
<td>0.85</td>
</tr>
</tbody>
</table>

 probabably was the result of agricultural field abandonment and forest succession as suggested by others (Keller and Scallan 1999, Betts et al. 2007). Similarly, Bart et al. (1995) found an increase in forest cover from 1963 to 1988 within 280 m of roads in western Ohio. Many agricultural fields may have been abandoned during the early time period, but the successional woody vegetation was not distinguishable from active agricultural fields on aerial photographs. Sufficient time had elapsed by the middle time period for abandoned agricultural fields to develop into early stage forests that could be differentiated on aerial photographs, but these young forests were likely less suitable Cerulean Warbler habitat. Young forests consist mainly of shrubs and pole-sized trees, lacking the large mature trees (Hamel 2000b) and horizontal and vertical structural diversity that Cerulean Warblers prefer (Weakland and Wood 2005, Perkins 2006), although young forests are not

TABLE 4. Land cover and fragmentation metrics based on 1992 and 2001 NLCD and Cerulean Warbler detections for 1990-1994 and 1999-2003 for 1,375 stops (df = 1,346), and for 344 presence-only stops (df = 319) along 28 BBS routes in West Virginia, Ohio, and Kentucky (FF edge density = Forest-forest edge density, FNF edge density = Forest-nonforest edge density).

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</tr>
</thead>
<tbody>
<tr>
<td>Deciduous/Mixed forest</td>
<td>64.3 ± 0.8</td>
<td>59.4 ± 0.7</td>
<td>38.94</td>
<td>&lt;0.001</td>
<td>81.6 ± 1.0</td>
<td>74.4 ± 0.8</td>
<td>45.88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>3.3 ± 0.2</td>
<td>1.5 ± 0.1</td>
<td>161.09</td>
<td>&lt;0.001</td>
<td>3.8 ± 0.3</td>
<td>0.9 ± 0.2</td>
<td>125.09</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Non-forest</td>
<td>32.4 ± 0.8</td>
<td>39.1 ± 0.7</td>
<td>79.08</td>
<td>&lt;0.001</td>
<td>14.6 ± 1.0</td>
<td>24.8 ± 0.8</td>
<td>110.07</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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</tr>
</thead>
<tbody>
<tr>
<td>Max forest patch (ha)</td>
<td>7.6 ± 0.1</td>
<td>8.0 ± 0.1</td>
<td>7.2</td>
<td>0.007</td>
<td>9.0 ± 0.2</td>
<td>9.7 ± 0.2</td>
<td>3.49</td>
<td>0.063</td>
</tr>
<tr>
<td>Core forest (%)</td>
<td>9.7 ± 0.3</td>
<td>9.1 ± 0.3</td>
<td>10.99</td>
<td>0.001</td>
<td>13.4 ± 0.5</td>
<td>13.5 ± 0.6</td>
<td>0.15</td>
<td>0.698</td>
</tr>
<tr>
<td>FF edge density (m/ha)</td>
<td>20.5 ± 0.4</td>
<td>7.5 ± 0.2</td>
<td>423.04</td>
<td>&lt;0.001</td>
<td>25.8 ± 0.7</td>
<td>9.2 ± 0.4</td>
<td>255.08</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>FNF edge density (m/ha)</td>
<td>187.8 ± 2.8</td>
<td>172.9 ± 1.8</td>
<td>11.34</td>
<td>0.001</td>
<td>159.9 ± 5.7</td>
<td>179.1 ± 3.2</td>
<td>54.24</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Cerulean Warbler detections/stop

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Average</td>
<td>0.08 ± 0.01</td>
<td>0.10 ± 0.01</td>
<td>2.54</td>
<td>0.11</td>
<td>0.31 ± 0.03</td>
<td>0.41 ± 0.03</td>
<td>5.45</td>
<td>0.03</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.19 ± 0.01</td>
<td>0.30 ± 0.02</td>
<td>1.81</td>
<td>0.18</td>
<td>0.76 ± 0.05</td>
<td>0.99 ± 0.05</td>
<td>5.60</td>
<td>0.02</td>
</tr>
</tbody>
</table>
completely avoided by Cerulean Warblers (Wood et al. 2005).

Cerulean Warbler abundance decreased during this same time period and their distribution became more restricted, changing from 15 to 3% of BBS stops. Regional BBS analyses (Sauer et al. 2008) found Cerulean Warblers declined from 1967 to 1982 in two of the three physiographic regions that comprised our study area (−4.8% in Ohio Hills, −5.2% in Cumberland Plateau). The lack of a positive response to increased young forest cover in breeding areas suggests events or conditions during migration or in wintering areas may contribute to population declines.

Recent Habitat and Cerulean Warbler Changes: 1982/1985 vs. 2000/2003.—The agriculture land cover lost from the middle to late periods was replaced by developed land cover for all stops and the set of stops at which Cerulean Warblers were detected. Agricultural fields appear to have been converted to development instead of being abandoned during this time period.

Core forest increased between the middle and late time periods with the all-stops data. Agricultural fields abandoned in the early time period and which were early stage deciduous/mixed forests by the middle time period, may have developed a more contiguous canopy cover by the late time period perhaps contributing to increases in core forest. Core forest is considered an important habitat characteristic for Cerulean Warblers (Oliarnyk 1996, Hamel 2000a); however, detections again decreased, but less than in the early versus middle time period. Regional BBS analyses (Sauer et al. 2008) similarly found a less steep decline in 1982–2003 in the Ohio Hills (−2.2) and the Cumberland Plateau (−2.1) physiographic regions.

Cerulean Warblers were detected at 27% of all stops in the middle and 30% in the late time period; however, more were detected per stop in the middle than the late time period (Table 3). The decrease in abundance but not distribution, the large decrease in abundance at stops with Cerulean Warbler presence, but lack of change in broad-scale fragmentation metrics considered important to Cerulean Warblers suggests there may be other small-scale factors (e.g., canopy gaps/heterogeneity) influencing population trends of Cerulean Warblers in breeding areas along the BBS routes examined.

Short-term Habitat and Cerulean Warbler Changes: 1992 vs. 2001.—Several NLCD land cover variables believed to be important to Cerulean Warblers declined from 1992 to 2001 at BBS stops. Deciduous/mixed forest declined and was replaced by non-forest land cover, primarily development, in both the all stops and presence-only analyses (Table 4).

The amount of deciduous/mixed forest and core forest was greater at stops where Cerulean Warblers occurred than at all stops. Cerulean Warbler abundance increased at presence-only stops and did not change at all stops despite the decline in deciduous/mixed forest. This, in concert with the increase in edge density, suggests microhabitat features within large, continuous deciduous/mixed forests also are important and provides support that, at a local scale, Cerulean Warblers are able to tolerate some edge habitat which may increase structural diversity in the canopy (Weakland and Wood 2005). The smaller amount of non-forest land cover at presence-only stops supports Cerulean Warbler avoidance of large-scale habitat disturbance (Wood et al. 2006).

Cerulean Warbler abundance may have increased at presence-only stops despite the decrease in deciduous/mixed forest and forest-forest edge density because their density increased in the remaining suitable habitat. A key habitat factor for Cerulean Warblers includes interior, unfragmented forests (Oliarnyk 1996, Hamel 2000a); however, there was little interior forest (9% for all stops and 13% for presence-only stops) in 2001 within 300 m of BBS stops. The maximum size forest patches within 300 m of a BBS stop increased for presence-only stops and all stops in our study area (Table 4), and were sufficiently large to contain several Cerulean Warbler territories (range = 0.21 ha [Roth 2004] to 1.04 ha [Oliarnyk and Robertson 1996]).

Cerulean Warbler detections did not change between 1992 and 2001 across all 1,375 BBS stops examined (Table 4); they were detected at 14% of all stops in 1992 and 17% in 2001. Sauer et al. (2008) reported declines of 4.1–6.8% during this time period for the three physiographic regions intersecting our study area. This disparity in trends may relate to which routes were included. We used data from 28 BBS routes because of lack of stop-level GPS coordinates and routes that were run inconsistently, whereas Sauer et al’s. (2008) trend analysis was based on 75 routes. Additionally, we focused on the core breeding range of Cerulean Warblers (Fig. 1), whereas Sauer et al. (2008) included more BBS routes near the periphery of the range.
Trends in Cerulean Warbler populations did not relate well to forest metrics, and loss of suitable forested habitat is still considered a major cause for Cerulean Warbler population declines in the core breeding range (Hamel et al. 2004). Our study illustrates the potential importance of microhabitat features such as small, isolated canopy gaps (Perkins 2006) that we were unable to detect with our coarse land cover analysis. Broad habitat features such as deciduous/mixed forest and forest-forest edge density decreased over time, while Cerulean Warbler detections increased, but none of these habitat variables accounted for canopy gaps or vegetation structure.

ACKNOWLEDGMENTS

We thank the US Fish and Wildlife Service, West Virginia Division of Natural Resources, National Fish and Wildlife Foundation, and the National Council for Air and Stream Improvement for financial support. We especially thank Keith Panek and Dave Ziółkowski, national coordinators of the Breeding Bird Survey, for access to and assistance with BBS data. We thank the many BBS observers whose participation was instrumental to the success of our study. Matthew Shumar, Molly McDermott, Jackie Strager, Brandon Miller, and Sandy Taylor helped with data collection and organization. Fekedeign Desta provided statistical support and Michael Strager provided logistical and technical support. The West Virginia Division of Natural Resources and Kentucky Department of Fish and Wildlife Resources provided off-road point-count data. Michael Strager, Keith Panek, and Dan McAuley provided valuable comments on this manuscript. Mention of trade names or commercial products does not imply endorsement by the U.S. Government.

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FISHERY DISCARDS AND INCIDENTAL MORTALITY OF SEABIRDS ATTENDING COASTAL SHRIMP TRAWLERS AT ISLA ESCONDIDA, PATAGONIA, ARGENTINA

CRISTIAN JAVIER MARINAO1,2 AND PABLO YORIO2

ABSTRACT.—We evaluated seabird attendance and incidental mortality at coastal trawl vessels targeting Argentine red shrimp (Pleoticus muelleri) in the Isla Escondida fishing area, Argentina, during 2006–2007 and 2007–2008. Eight seabird species attended vessels, and the most frequent and abundant seabird (percent occurrence, mean number per haul) in the two seasons was the Kelp Gull (Larus dominicanus) (100%, 112.3, and 100%, 263.4, respectively), followed by the Black-browed Albatross (Thalassarche melanophris) (85%, 17.6, and 90%, 32.4, respectively). Eleven Magellanic Penguins (Spheniscus magellanicus) and one Imperial Shag (Leucocarbo atriceps) were killed in nets with a mean capture rate of 0.003 and 0.0003 birds per haul, respectively. The estimated total number of birds killed was 53 penguins and five shags considering the total number of hauls made by the fishery in the two seasons. No contacts between seabirds and warp cables were recorded. Coastal shrimp vessels generally operated between 15 and 20 km offshore, at a mean distance from the main Kelp Gull colony (Punta Tumbo) of 43.9 km. At least 100 fish and invertebrate species were discarded, mostly Argentine hake (Merluccius hubbsi). Total amount discarded per season by this coastal fishery in the two seasons was estimated at 3,284 and 6,590 tonnes, respectively. The coastal shrimp fishery in the Isla Escondida area appears to have a small impact on seabirds in terms of incidental mortality but provides significant amounts of supplementary food during the breeding season of the Kelp Gull. Received 27 January 2011. Accepted 22 May 2011.

Commercial fishing can generate important alterations in marine ecosystems and have important effects on top predators (Pauly et al. 2005). Seabirds are among the top predators which most regularly interact with fisheries, and can be negatively affected as a result of incidental capture and competition for common resources (Duffy and Schneider 1994, Tasker et al. 2000, Monteverchi 2002). In addition, due to the low selectivity of fishing gear, trawl fisheries discard large amounts of fish and invertebrates (Alverson et al. 1994) which are used by many organisms, including seabirds (Garthe et al. 1996, Furness et al. 2007). Discard consumption at sea is currently an important component of the trophic ecology of many seabird species (Camphuysen 1994, Garthe and Hüppop 1994), and many studies show that provision of this supplementary food may affect at-sea distribution, body condition, individual survival, and breeding success (e.g., Ryan and Moloney 1988, Hudson and Furness 1989, Oro 1999, Hüppop and Wurm 2000, Grémillet et al. 2008). In addition, it has been argued that discard use can contribute to population growth of some species of seabirds (Furness 2003), although there is some controversy (Camphuysen and Garthe 1999, Thompson 2006). Attraction to vessels may also result in incidental mortality from drowning in fishing gear and/or collisions with warp cables (Weimerskirch et al. 2000, González-Zevallos and Yorio 2006, Sullivan et al. 2006, Watkins et al. 2008, Fuevero et al. 2011).

Commercial fishing in France can generate important alterations in marine ecosystems and have important effects on top predators (Pauly et al. 2005). Seabirds are among the top predators which most regularly interact with fisheries, and can be negatively affected as a result of incidental capture and competition for common resources (Duffy and Schneider 1994, Tasker et al. 2000, Monteverchi 2002). In addition, due to the low selectivity of fishing gear, trawl fisheries discard large amounts of fish and invertebrates (Alverson et al. 1994) which are used by many organisms, including seabirds (Garthe et al. 1996, Furness et al. 2007). Discard consumption at sea is currently an important component of the trophic ecology of many seabird species (Camphuysen 1994, Garthe and Hüppop 1994), and many studies show that provision of this supplementary food may affect at-sea distribution, body condition, individual survival, and breeding success (e.g., Ryan and Moloney 1988, Hudson and Furness 1989, Oro 1999, Hüppop and Wurm 2000, Grémillet et al. 2008). In addition, it has been argued that discard use can contribute to population growth of some species of seabirds (Furness 2003), although there is some controversy (Camphuysen and Garthe 1999, Thompson 2006). Attraction to vessels may also result in incidental mortality from drowning in fishing gear and/or collisions with warp cables (Weimerskirch et al. 2000, González-Zevallos and Yorio 2006, Sullivan et al. 2006, Watkins et al. 2008, Fuevero et al. 2011).

The use of fishing discards has been evaluated in several regions worldwide (Abrams 1983, Furness et al. 1988, Blaber and Wassenberg 1989, Thompson 1992, Oro and Ruiz 1997, Branco 2001, Garthe and Scherp 2003, Wickliffe and Jodice 2010). Seabird attendance and discard use in Argentina has been analyzed for several trawl fisheries (Yorio and Caille 1999, Bertellotti and Yorio 2000b, González-Zevallos and Yorio 2006), including the coastal fishery that operates in the Isla Escondida area, Patagonia. However, information available for this fishery includes only identification and frequency of occurrence of attending seabirds (Yorio and Caille 1999, Bertellotti and Yorio 2000b, González-Zevallos and Yorio 2006), including the coastal fishery that operates in the Isla Escondida area, Patagonia. However, information available for this fishery includes only identification and frequency of occurrence of attending seabirds (Yorio and Caille 1999) and further information is required to adequately interpret the magnitude of the seabird-fishery interaction. One of the main species taking advantage of discards at this and other Patagonian coastal fisheries is the Kelp Gull (Larus dominicanus) (Yorio and Caille 1999, Bertellotti and Yorio 2000b, González-Zevallos and Yorio 2006), Kelp Gull populations have increased since the 1980s, and it has been suggested that human-derived food sources have been an important factor (Yorio et
al. 1998a, Yorio et al. 2005). Kelp Gulls and other gulls worldwide can negatively affect other coastal birds through predation, competition for breeding space and kleptoparasitism, and generate conflicts with human populations (Yorio et al. 1998a, Frere et al. 2000, Albarnaz et al. 2007). Thus, knowledge of how seabirds use fishery waste provided by the Isla Escondida coastal fishery will contribute to ecosystem-based fisheries management, and provide valuable information on the contribution of supplementary food to an expanding gull population. The goal of our study was to analyze the interactions between seabirds and coastal trawl vessels targeting Argentine red shrimp (*Pleoticus muelleri*) in the Isla Escondida fishing area with emphasis on the Kelp Gull. We identified the species composition of seabirds attending vessels during two fishing seasons, quantified their relative abundance in relation to the fishing season and stages of fishing operations, quantified mortality as a result of incidental capture of birds attracted to the vessels to make use of fishery waste, and assessed the quantity and composition of discards potentially available to seabirds.

**METHODS**

**Study Area and Characteristics of the Fishery.**—The study area comprised the coastal waters up to 22.2 km offshore under the jurisdiction of Chubut Province from 43° 20' S to 44° 02' S ("Isla Escondida" fishing area) (Fig. 1). The coastal trawl fishery operating at Isla Escondida targets Argentine red shrimp or Argentine hake (*Merluccius hubbsi*) depending on resource availability and market demands, but we only evaluated shrimp vessels which were responsible for about 80% of the effort of the fishery during the study years. The fishery consists of 35–40 coastal ice trawlers, 21 m long, which operate from November to March. Shrimp vessels remain 1 or 2 days in the fishing area, making on average seven hauls per day lasting on average 1 hr each (Secretaria de Pesca de la Provincia de Chubut, unpubl. data). Shrimp are sorted on deck, and non-commercial sizes and bycatch species are discarded overboard either as a constant stream or in pulses depending on the composition of the catch. The study area includes three breeding sites (Fig. 1) of seabirds which regularly interact with coastal fisheries in Patagonia: Punta Tombo, Punta
Clara, and Escondida Island (Yorio et al. 1998b). Punta Tombo (44° 02' S, 65° 11' W) is one of the main breeding sites of Magellanic Penguins (Spheniscus magellanicus; 175,000 pairs) on the Patagonian coast, and has the main Kelp Gull colony in this coastal sector (5,400 pairs). Other species breeding at this location include Imperial Shag (Leucocarbo atriceps) and Brown Skua (Stercorarius antarcticus). Punta Clara (43° 58' S, 65° 15' W), 7 km north of Punta Tombo, includes 70,000 Magellanic Penguin and 40 Kelp Gull pairs. About 500 Imperial Shag pairs breed at Escondida Island (43° 43' S, 65° 17' W). Kelp Gulls in the study area start laying in early November, most eggs hatch in early January, and chicks fledge during February (Bertellotti and Yorio 1999). Magellanic Penguins arrive at breeding sites in early September, start laying in early October, eggs start hatching in early November, most chicks fledge in February, and the last adults leave the colony for their winter migration during April (Boersma et al. 1990). Imperial Shags arrive at the Punta Tombo colony during August, start laying in late October, eggs hatch in late November, and the last chicks fledge in late March (Malacalza 1984).

Species and Abundance of Seabirds Attending Vessels.—We gathered information on board 15 coastal shrimp trawlers (38% of the fishing fleet) during regular fishing operations from December 2006 to March 2007 and from December 2007 to February 2008. We gathered information during each trip for only one haul per day during midday, totaling 20 hauls (20 fishing days) in each of the fishing seasons. More than 80% of hauls in each season corresponded to the months of January and February, i.e., during seabird incubation and chick rearing. We identified seabirds attending the vessel during all hauls to species level and recorded their numbers. We made counts during a 10-min observation period from the stern of the vessel, only once at the beginning of discarding (sorting and discarding fish while towing the net), covering up to a 100-m radius. We also gathered information during haulback (lifting of the net to cover up to a 100-m radius). We also gathered information during haulback (lifting of the net to cover up to a 100-m radius). We also gathered information during haulback (lifting of the net to cover up to a 100-m radius).

Seabird Incidental Mortality.—We obtained information on incidental captures of seabirds in nets, including species’ identity and number of birds caught in each haul, from the data base of the On-board Observer Program of Chubut Province, of which the first author was part, for the 2006–2008 period (n = 3,149 hauls). In addition, for the 40 hauls in which we evaluated seabird attendance, we quantified their interaction with warp cables to examine the occurrence of contacts and associated mortality. Observations at each haul were made from the stern of the vessel during the period when fish were discarded (~10 min to 3 hrs, depending on size of the catch).

Spatial Distribution of the Fishery and Discard Composition.—We mapped the distribution of hauls in both fishing seasons obtained from the data base of the On-board Observer Program of Chubut Province using ArcView 3.2 (ESRI 1998) to assess the spatial and temporal distribution of operating shrimp vessels. We present haul distribution as density maps on a 5 × 5 km grid. We calculated the distances of each haul to Punta Tombo, Punta Clara, and Escondida Island using the same software.

We estimated the total amount discarded by the coastal trawl fishery in each study year extrapolating the mean value (in kg) corresponding to hauls evaluated by the On-board Observer Program during the entire fishing season (Nov to Mar) to the total number of hauls made by the fishery during that period. We estimated the total number of hauls made by the fishery by dividing the declared catch in the study period (Secretaría de Agricultura, Ganadería, Pesca y Alimentación de Argentina, unpubl. data) by the mean catch of observed hauls (On-board Observer Program of Chubut Province, unpubl. data). We estimated the amounts discarded per haul subtracting the retained catch from the total catch, and obtained the total catch for each haul averaging the independent estimates made by the vessel captain and the on-board observer.

We obtained information on the catch composition by shrimp vessels from the data base of the On-board Observer Program of Chubut Province, totaling 1,219 hauls corresponding to the months of December to March and December to February in the 2006–2007 and 2007–2008 fishing seasons, respectively. Personnel of the On-board Observer Program estimated the abundance of caught prey in each haul and assigned them to one of four

Vessels.—We gathered information on board 15 coastal shrimp trawlers (38% of the fishing fleet) during regular fishing operations from December 2006 to March 2007 and from December 2007 to February 2008. We gathered information during each trip for only one haul per day during midday, totaling 20 hauls (20 fishing days) in each of the fishing seasons. More than 80% of hauls in each season corresponded to the months of January and February, i.e., during seabird incubation and chick rearing. We identified seabirds attending the vessel during all hauls to species level and recorded their numbers. We made counts during a 10-min observation period from the stern of the vessel, only once at the beginning of discarding (sorting and discarding fish while towing the net), covering up to a 100-m radius. We also gathered information during haulback (lifting of the net to cover up to a 100-m radius). We also gathered information during haulback (lifting of the net to cover up to a 100-m radius). We also gathered information during haulback (lifting of the net to cover up to a 100-m radius). We also gathered information during haulback (lifting of the net to cover up to a 100-m radius).
TABLE I. Frequency of occurrence (%F) and abundance (mean ± SD; range in parentheses) per haul of seabirds attending coastal shrimp trawlers in the Isla Escondida area, Argentina, during fishing seasons of 2006-2007 (n = 20 hauls) and 2007-2008 (n = 20 hauls). (*) Species that breed in Chubut.

<table>
<thead>
<tr>
<th>Species</th>
<th>2006-2007</th>
<th>2007-2008</th>
<th>Mann-Whitney</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%F</td>
<td>Abundance</td>
<td>%F</td>
</tr>
<tr>
<td>Kelp Gull* (Larus dominicanus)</td>
<td>100</td>
<td>112.3 ± 68.4 (30-270)</td>
<td>100</td>
</tr>
<tr>
<td>Black-browed Albatross</td>
<td>85</td>
<td>17.6 ± 18.0 (0-60)</td>
<td>90</td>
</tr>
<tr>
<td>White-chinned Petrel* (Procellaria aequinoctialis)</td>
<td>50</td>
<td>5.9 ± 9.5 (0-30)</td>
<td>90</td>
</tr>
<tr>
<td>Imperial Shag* (Leiocephalus atriceps)</td>
<td>75</td>
<td>7.3 ± 15.3 (0-70)</td>
<td>90</td>
</tr>
<tr>
<td>Magellanic Penguin* (Spheniscus magellanicus)</td>
<td>30</td>
<td>0.8 ± 1.3 (0-4)</td>
<td>55</td>
</tr>
<tr>
<td>Southern Giant Petrel* (Macronectes giganteus)</td>
<td>45</td>
<td>1.1 ± 1.8 (0-6)</td>
<td>25</td>
</tr>
<tr>
<td>Great Shearwater (Puffinus gravis)</td>
<td>5</td>
<td>0.3 ± 1.1 (0-5)</td>
<td>45</td>
</tr>
<tr>
<td>Sooty Shearwater (P. griseus)</td>
<td>30</td>
<td>1.6 ± 3.2 (0-11)</td>
<td>0</td>
</tr>
</tbody>
</table>

categories, based on their percent representation in the catch: (1) dominant (Do): >50% of the catch, its presence gives the general appearance to the catch; (2) abundant (Ab): between 25 and 50% of the catch, its presence is easily detected; (3) common (Co): between 5 and 25% of the catch, its presence is detected when paying attention and searching through the catch; and (4) rare (Ra): <5% of the catch, only a few individuals.

Similarly, the fate of species caught in each haul was assigned to one of three categories: (1) totally discarded (TDi), (2) totally retained (TRe), and (3) partially retained (PRe). We defined the frequency of occurrence for each caught species as the percentage of hauls in which each species in the catch was observed.

RESULTS

Species and Abundance of Seabirds Attending Vessels.—Eight seabird species were recorded foraging upon discards from the coastal shrimp fishery in the Isla Escondida area (Table 1). The most frequent and abundant seabird was the Kelp Gull, which was present at all hauls evaluated in both years, followed by Black-browed Albatross (Thalassarche melanophris) (Table 1). Flock size of both species varied throughout the fishing season, reaching 270 and 1,700 Kelp Gulls, and 60 and 210 Black-browed Albatrosses in the two study seasons, respectively (Fig. 2). Young Kelp Gulls during the 2007-2008 fishing season were recorded at 85% of hauls, but in significantly lower numbers than adults (X ± SD, 44.2 ± 88.0; range = 0-400; n = 20 vs. 219.3 ± 300.8; range = 25-1,300; n = 20, respectively; Wilcoxon test W = 0.002, P < 0.0001).

Frequencies of occurrence of White-chinned Petrels (Procellaria aequinoctialis) and Imperial Shags, particularly during the 2007-2008 fishing season, were relatively high, although abundances were relatively low (Table 1). The highest number of White-chinned Petrels was recorded during the 2007-2008 fishing season (55 individuals). When present, Imperial Shag numbers varied between 1 and 100 individuals (Fig. 2). Magellanic Penguins and Great Shearwaters (Puffinus gravis) during 2007-2008 had frequencies of occurrence <50%, but their abundances were low (Table 1). Southern Giant Petrels (Macronectes giganteus) and Sooty Shearwaters (P. griseus) had low frequencies of occurrence and only a few individuals per haul.

The mean numbers of Magellanic Penguins, Southern Giant Petrels, Great Shearwaters, and Sooty Shearwaters were significantly higher during 2007-2008 than in 2006-2007 (Table 1). Only the Kelp Gull and Black-browed Albatross of the four most frequent and abundant species attending vessels had significantly higher numbers during discarding than haulback (Table 2). Numbers of Kelp Gulls and Black-browed Albatrosses attending a vessel were significantly higher when there were only one or two vessels operating simultaneously than when there were three or more (Kelp Gulls: 569.5 ± 623.1 vs. 132.2 ± 69.9, Mann-Whitney U = 82, P = 0.03; Black-
Incidental Seabird Mortality.—Fifteen individuals were caught in 3,149 hauls evaluated by the On-board Observer Program, of which three were able to escape alive. The 12 birds killed included 11 Magellanic Penguins and one Imperial Shag, resulting in a mean mortality rate of 0.003 and 0.0003 birds per haul, respectively. Extrapolating this value to the total number of hauls by the Isla Escondida fishery in the 2 years \( (n = 15,232 \text{ hauls}) \), we estimated a total of 53 penguins and 5 shags were killed in nets. These estimates are an indication of the actual numbers of birds killed. No contacts (fatal and non-fatal) between seabirds and warp cables were recorded \( (n = 40 \text{ hauls}) \).

Spatial Distribution of the Fishery and Discard Composition.—Hauls were distributed between 43° 30' and 44° 10' S during both study years with most occurring between 43° 65' and 43° 75' S.

Hauls were generally between 15 and 20 km offshore, although in January 2007 some hauls were <5 km from the coast (Fig. 3). Coastal shrimp vessels operated at a mean distance from Punta Tombo of 43.9 ± 10.0 km (range = 7.1–73.3; n = 1,219), while mean distance to Punta Clara was 38.0 ± 9.5 km (range = 1.5–67.5; n = 1,219). Mean distance between operating vessels and the Imperial Shag colony at Escondida Island was 20.4 ± 6.5 km (range = 2.8–46.6; n = 1,219). Distances to these colonies decreased significantly as the breeding season progressed (Table 3).

At least 100 species were discarded in the 1,219 evaluated hauls, of which 48% were fish (Table 4; only species with >20% of frequency of occurrence are shown). Argentine hake was recorded in 76% of hauls. Hake was totally retained in only 0.7% of hauls, while it was discarded (74.3%) or partially retained (25.0%) in the rest of the hauls. Several of the remaining discarded species were present in the catch in relatively high frequencies, but were categorized as rare in over 83% of hauls (Table 4). Thus, the Argentine hake was the main species discarded. The estimated amount of discards per haul was significantly higher in the 2007–2008 than in the 2006–2007 fishing seasons (513.46 ± 576.43 kg; range = 0–8,000; n = 1,152 vs. 305.05 ± 382.86 kg; range = 0–2,490; n = 469) (Mann-Whitney U = 285,847.50 P < 0.0001). Total amount discarded by this coastal trawl fishery was estimated at 3,284 tonnes in 2006–2007 and 6,590 tonnes in 2007–2008.

DISCUSSION

Eight seabird species attended shrimp coastal trawlers operating in the Isla Escondida fishing area, although the seabird assemblage was dominated by the Kelp Gull and Black-browed albatross. Species composition differed from that reported in a previous study in the same fishing area during the mid 1990s, when 16 seabird species were recorded taking advantage of discards (Yorio and Caille 1999). The reason for this difference is not clear, but five of the species not recorded during the present study (Cape Petrel...
TABLE 3. Mean distance (± SD; range in parentheses) between seabird colonies and hauls by vessels in the Isla Escondida area, Argentina, during the 2006–2007 and 2007–2008 fishing seasons.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Fishing season</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Kruskal-Wallis test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Punta Tombo</td>
<td>2006–2007</td>
<td>56.0 ± 1.4 (52.6–51.3)</td>
<td>47.9 ± 8.6 (7.1–11.9)</td>
<td>43.2 ± 3.1 (33.8–58.0)</td>
<td>H = 90.79; P &lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>2007–2008</td>
<td>50.6 ± 8.3 (31.2–73.3)</td>
<td>39.8 ± 8.9 (11.6–61.6)</td>
<td>36.9 ± 8.7 (8.2–45.8)</td>
<td>H = 244.71; P &lt; 0.0001</td>
</tr>
<tr>
<td>Punta Clara</td>
<td>2006–2007</td>
<td>49.8 ± 1.4 (46.2–51.0)</td>
<td>41.3 ± 8.7 (1.5–65.9)</td>
<td>37.4 ± 3.1 (26.8–52.1)</td>
<td>H = 55.81; P &lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>2007–2008</td>
<td>44.4 ± 8.1 (25.9–67.5)</td>
<td>34.2 ± 8.5 (10.1–55.9)</td>
<td>31.4 ± 7.8 (6.2–39.5)</td>
<td>H = 244.34; P &lt; 0.0001</td>
</tr>
<tr>
<td>Escondida Island</td>
<td>2006–2007</td>
<td>26.7 ± 13.1 (23.4–27.9)</td>
<td>18.2 ± 9.1 (2.8–42.7)</td>
<td>20 ± 3.1 (7.7–31)</td>
<td>H = 47.17; P &lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>2007–2008</td>
<td>23.3 ± 6.3 (13.2–34.8)</td>
<td>20.1 ± 4.2 (13.7–46.6)</td>
<td>H = 69.68; P &lt; 0.0001</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 4. Catch composition in the coastal shrimp fishery in the Isla Escondida area, Argentina, during the 2006–2007 and 2007–2008 fishing seasons (n = 1,219 hauls). Only species with >20% of frequency of occurrence (%F) are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Abundance</th>
<th>Fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>requent shrimp (Pleoticus muelleri)</td>
<td>92.9</td>
<td>68.9</td>
</tr>
<tr>
<td>Argentine hake (Merluccius hubbsi)</td>
<td>76.0</td>
<td>0.6</td>
</tr>
<tr>
<td>Flatfish (Paralichthyidae)</td>
<td>83.6</td>
<td>0.3</td>
</tr>
<tr>
<td>Squid (Loligo spp.)</td>
<td>75.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Butterfish (Scombrotus brasiliensis)</td>
<td>60.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Brazilian flathead (Perichthys brasiliensis)</td>
<td>59.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Rays (Rajidae)</td>
<td>54.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Argentine seabass (Acanthistius brasiliensis)</td>
<td>48.7</td>
<td>0.2</td>
</tr>
<tr>
<td>Parona leatherjacket (Parona signata)</td>
<td>46.7</td>
<td>3.0</td>
</tr>
<tr>
<td>Castaneta (Nomadactylus bergi)</td>
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<td>Argentine seventh spine (Illex argentinus)</td>
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<tr>
<td>Elephant fish (Callorhinchus callorhinchus)</td>
<td>35.5</td>
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<tr>
<td>Sharks (Triakidae, Squididae, and Squatinidae)</td>
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<td>Banded eel (Romeo brasiliensis)</td>
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</tr>
<tr>
<td>Argentine sandpiper (Pseudopercis semifasciata)</td>
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</tr>
<tr>
<td>Brazilian sandpiper (Pinguipes brasiliensis)</td>
<td>23.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Argentine anchovy (Engraulis anchoita)</td>
<td>20.0</td>
<td>6.3</td>
</tr>
</tbody>
</table>

* Dominant >50% of the catch, its presence gives the general appearance to the catch.
* Abundant Between 25 and 50% of the catch, its presence is easily detected.
* Common Between 5 and 25% of the catch, its presence is detected when paying attention and searching through the catch.
* Rare <5% of the catch, only a few individuals.
* Totally discarded.
* Partially retained.
* Rarely retained.
The regular presence of Kelp Gulls in this and other fisheries in the region is the result of its generalist and opportunistic feeding habits, which are mainly characterized by coastal feeding and regular use of human-derived food sources (Bertellotti and Yorio 1999, Yorio et al. 2005).

Black-browed Albatrosses are also regularly present at trawl fisheries in the southwest Atlantic (Thompson 1992, Thompson and Riddy 1995, Yorio and Caille 1999, González-Zevallos and Yorio 2006, Bugoni et al. 2011, Favero et al. 2011) and in other regions of the Southern Hemisphere (Abrams 1983, Ryan and Moloney 1988, Petyt 1995). Mean abundance in the Isla Escondida area was relatively lower than observed at coastal trawlers in Golfo San Matías and Golfo San Jorge, Patagonia (Yorio and Caille 1999). In contrast, both abundance and frequency of occurrence of Black-browed Albatross at hake and shrimp high-sea trawlers operating in Golfo San Jorge were larger, on occasions reaching numbers per haul three times greater than recorded at Isla Escondida (González-Zevallos et al. 2007, González-Zevallos et al. 2011). This may be the result of larger amounts of fishery waste discarded overboard and/or the greater distances offshore at which the high-seas trawlers operate (González-Zevallos et al. 2011).

Only the Kelp Gull and Black-browed Albatross of the most abundant seabird species attending vessels had significantly higher abundances during discarding activities. Differences among species may relate to their feeding behaviors. Kelp Gulls and Black-browed Albatrosses obtain food mainly through surface feeding, while Imperial Shags and White-chinned Petrels do so by diving (González-Zevallos and Yorio 2006). Thus, diving species start obtaining prey directly from the net or capturing those that fall off the net as it reaches the surface during haulback, while gulls and albatrosses increase in numbers as a result of their attraction when prey start to be available during discarding. Birds were often observed moving among vessels as in other fisheries in Patagonia (Bertellotti and Yorio 2000b, González-Zevallos and Yorio 2006).

Argentine hake was the main discard component, as it was one of the most frequently caught species and was totally retained on board in only a few cases. Previous studies in Patagonia have shown that Argentine hake is one of the most taken species by adult and young Kelp Gulls feeding on discards (Bertellotti and Yorio 2000b, González-Zevallos and Yorio 2006, González-Zevallos and Yorio 2011). The Argentine hake is a demersal fish not normally available to seabirds that surface-feed, such as the Kelp Gull, and it constitutes an important supplementary food resource. The use of this food may be advantageous for Kelp Gull breeding success and survival, as several studies have shown that fish are important for both egg formation and chick growth of gulls (Pierotti and Annett 1991, Bolton et al. 1992) and may favor long-term breeding performance (Annett and Pierotti 1999).

The fishing season in the Isla Escondida area coincides with the Kelp Gull’s breeding season at Punta Tombo and Punta Clará. However, discards were not uniformly available within the known foraging range of this species during the breeding season. Several studies have shown the relative contribution of supplementary food in gull diets is related to accessibility of these resources (Oro 1995, Bertellotti and Yorio 1999, Pedrocchi et al. 2003, Duhem et al. 2005, Ramos et al. 2009). Thus, the extent of discard use and its potential effect on breeding success in a given locality would depend on the spatio-temporal pattern of vessel distribution. Discard availability could be particularly beneficial for young Kelp Gulls which, in contrast to breeders, are not spatially constrained to the nest during foraging activities. Young Kelp Gulls were recorded in most hauls during this study. Young individuals are in general less efficient than adults in obtaining food (Burger 1987, Hockey and Steele 1990, Bertellotti and Yorio 2000a). Thus, discard use may have an important influence on survival, particularly during February and March when young gulls start to become independent from their parents.

Seabird attraction to vessels to make use of discards may lead to an increase in mortality resulting from interaction with fishing gear (González-Zevallos and Yorio 2006, Sullivan et al. 2006, Watkins et al. 2008). Incidental mortality in nets was associated with diving species such as Magellanic Penguin and Imperial Shag, most likely because these species dive to take prey directly from the net during haulback increasing their chances of becoming entangled. Studies at Punta Tombo show that breeding Magellanic Penguins during December and January forage in relatively coastal areas at mean distances of...
Isla Escondida fishery and seabird populations. An integrated view of the interaction between the fishery and seabirds should be assessed in conjunction with the effects of shrimp trawlers to obtain a more integrated view of the interaction between the fishery and seabirds at Isla Escondida. The fishery in the Isla Escondida area can also target Argentine hake, and changes in both net and mesh sizes, and in the characteristics of the fishing operation may result in differences in composition and amounts of discards. These variables can affect the composition and abundance of seabirds attending vessels, the way and effectiveness at which each species uses available discards, and their probability of being killed in fishing gear (Arcos and Oro 2002, Furness et al. 2007, Favero et al. 2011). Fishing for Argentine red shrimp and Argentine hake may often coincide in time and space. Thus, the effects of coastal hake trawlers on seabirds should be assessed in conjunction with those of shrimp trawlers to obtain a more integrated view of the interaction between the Isla Escondida fishery and seabird populations.

ACKNOWLEDGMENTS

We thank Centro Nacional Patagónico (CONICET) for institutional support, Secretaría de Pesca de la Provincia de Chubut for logistical support and for providing data from the On-board Observer Program, and the Wildlife Conservation Society for financial support. We especially thank M. E. Gonzaga, D. R. González-Zevallos, N. D. Boveon, P. O. Dell’Arciprete, J. R. C. Saravia, and the captains and crews of the coastal shrimp trawlers for their help and advice.

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GENDER ASSIGNMENT OF WESTLAND PETRELS (PROCELLARIA WESTLANDICA) USING LINEAR DISCRIMINANT FUNCTION ANALYSIS

TODD J. LANDERS,1,2,3,5 TODD E. DENNIS,2 AND MARK E. HAUBER2,4

ABSTRACT.—Rapid classification of a study subject’s gender is critical for many ecological, behavioral, and conservation projects. We evaluated sexual-size dimorphism of adult Westland Petrels (Procellaria westlandica), a large nocturnal colony-nesting seabird, using linear discriminant function analysis and compared our results to birds classified using standard DNA gender identification techniques. The results revealed a strong pattern of sexual dimorphism (Wilk’s Lambda = 0.43, F7,29 = 5.6, P < 0.001) in the standard discriminant function analysis despite an unbalanced sex ratio in our sample of adults captured at the breeding colony. Minimum bill depth and head length, of the seven morphometric characters we measured, successfully assigned the correct gender to 95% of all individuals sampled (n = 37). We provide a canonical classification function of morphological traits that may be used in the field to rapidly differentiate adult females and males of this rare petrel species. Received 6 September 2010. Accepted 21 May 2011.

Both cryptic and measurable sexual differences, including size dimorphism, are common in birds (Dale et al. 2007), but assignment of differences between females and males based on measurements needs to be confirmed with independent techniques (e.g., using anatomical or molecular methods) (Kahn et al. 1998, Daniel et al. 2007, Igic et al. 2010). Rapid, in-hand identification of gender may be especially critical for behavioral and conservation studies, including balanced representation of females and males in tracking studies involving expensive tagging equipment (e.g., Landers et al. 2011).

The Westland Petrel (Procellaria westlandica: Procellariidae), one of the largest burrowing procellariform seabirds (~1.2 kg), is endemic to Westland, New Zealand, breeding annually during the austral winter in a number of distinct subcolonies within Paparoa National Park (Marchant and Higgins 1990, Waugh et al. 2006). This species is nocturnally active when at its colony, and uses an obligate, biparental breeding strategy (Brooke 2004). Westland Petrels are listed as Vulnerable by the International Union for the Conservation of Nature (IUCN 2010), and has been identified by the New Zealand Department of Conservation as a research priority (Taylor 2000).

Little is known about how male and female Westland Petrels differ morphologically or behaviorally, which is critical for current and future ecological studies and conservation management of this species. Westland Petrel females and males are alike in having monochromatic plumage (Marchant and Higgins 1990). Previous studies of museum specimens suggested males may be larger (Marchant and Higgins 1990; J. A. Bartle, pers. comm.), but a formal assessment of the extent and magnitude of potential differences is needed. Our goal was to evaluate sexual-size dimorphism in Westland Petrels using discriminant function analysis (Fisher 1936, Dechaume-Moncharmont et al. 2011). Specific objectives were to: (1) evaluate if females and males could be reliably identified using several commonly measured morphometric characters, (2) identify which characters measured best differentiate females and males, and (3) develop canonical classification functions to accurately and rapidly classify females and males from morphological measurements taken in the field.

METHODS

Field Procedures.—Thirty-seven adult Westland Petrels were captured from their nest burrows within 1 week, during the early breeding season in April 2010 at the Scotchman’s Creek colony (42°08.8′ S, 171°20.5′ E), Westland, New Zealand. A body feather sample was collected from each bird, placed in a plastic bag, and sent to the Equine Parentage and Animal Genetic Services Centre, Massey University, New Zealand, for commercial
molecular analysis using the CHD gene of the avian sex chromosomes (Kahn et al. 1998).

Morphometric Measurements.—Seven body measurements typically collected in ornithological, including seabird, studies (Guicking et al. 2004, Bourgeois et al. 2007, Thalmann et al. 2007) were taken (always from the left appendage for bilateral traits). These were: (1) head length (HL) from the cerebellum roof (= supraoccipital) to the edge of the feather implantation on the culmen, (2) bill length (BL) = exposed culmen from the tip of the hook to the edge of the feather implantation, (3) minimum bill depth (MBD) = minimum bill thickness of upper and lower mandibles measured vertically, (4) tarsus length (TL) = metatarsus length from the depression in the angle of the intertarsal joint to the base of the last complete scale before the toe diverges, (5) toe length (MTL) = middle toe length from the first scale of the middle toe to the base of the nail on this toe, (6) wing length (WL) = maximum flattened chord) and (7) body mass (BM). All measurements were made with digital slide calipers to the nearest 0.1 mm except wing length, for which a stopped wing-rule was used (to the nearest 0.1 cm), and mass where a handling bag and Pesola balance were used (measured to the nearest 5 g). We measured birds as a team to maximize consistency where one researcher (TJL) held the bird while the other (TED) took the measurements. Several repeat measures were taken for the first few birds to familiarize ourselves with the procedure (only the last set of measurements for each bird was used for analysis), after which all subsequent birds were measured only once.

Statistical Analyses.—We performed univariate t-tests of each morphometric character, and calculated the percentage of dimorphism between males and females (based on the molecular data) for each character measured as \[ \frac{(x_m - x_f)}{2} \cdot 100 \], where \( x_m \) and \( x_f \) are mean values for males and females, respectively (Holmes and Pitelka 1968). We used Pearson product-moment correlations to examine relationships among individual morphometric characteristics. We assessed whether the seven morphological characters collectively differed between females and males, using a one-way multivariate analyses of variance (MANOVA) with gender as the categorical factor and morphological characters as the dependent variables.

Linear discriminant function analyses (DFA) were used to identify which characteristic best differentiated females and males, and how accurately gender could be classified using the resulting canonical classification function. We performed a standard DFA using all characteristics, so they could be examined conjointly, and to facilitate comparisons with published studies on avian size dimorphism. We performed stepwise DFAs (both forward and backward) to evaluate the reliability of the results of the standard DFA. The results of all DFAs were similar, and we report only the canonical function from the standard DFA, as this was most comprehensive.

We tested the effectiveness of the standard DFA by a jackknife procedure, in which each individual was classified based on a discriminant function formulated when the focal individual was removed and the remaining individuals were used to calculate the function (Quenouille 1956, Lachenbruch and Mickey 1968, Genovart et al. 2003). The resulting canonical classification functions may be used to classify the gender of additional Westland Petrels by adding a bird’s morphometric measurements from the field into the female and male functions with the higher DF score predicting its gender. Partial eta-squared \( (\eta^2) \) values are also reported, which are defined as the proportion of total variation attributed to the factor, excluding other factors from the total non-error variation (Pierce et al. 2004). All statistical tests were conducted with STATISTICA 9 (StatSoft 2009).

RESULTS

Molecular analysis identified seven females and 30 males in our samples (binomial test with random expectation 50%: \( P = 0.098 \)). There was considerable variation in the magnitude and range of the differences between males and females in the seven morphological characteristics; males were consistently larger in all traits (Fig. 1). Unpaired t-tests revealed that males were significantly larger in head length, minimum bill depth, and body mass with gender explaining 35, 42, and 11% of the variation of these characteristics, respectively (Table 1). Several characters were positively inter-correlated within subjects (Table 2) as expected for size dimensions; however, there was no strong multicollinearity as \( r \) was at most 0.58 for any correlations. Generally, larger morphometric features (e.g., wing and head length) were related with body mass, and features of the head and bill were associated. Overall,
females and males differed (MANOVA; $F_{2,29} = 5.6, P < 0.001$) in morphometric features.

The standard discriminant function model was strongly significant (Wilks’ Lambda = 0.43, $F_{7,29} = 5.6, P < 0.001$). Its canonical discriminant function (Fig. 2) was defined primarily by variation in minimum bill depth and head length (factor loadings: MBD = 0.73, HL = 0.67, BM = 0.30, BL = 0.28, MTL = 0.26, WL = 0.22, TL = 0.18): MBD and HL were the only significant characters (MBD: $F_{1,34} = 17.6, P < 0.01$; HL: $F_{1,34} = 12.0, P < 0.01$). The stepwise DFAs yielded similar results (forward: Wilks’ Lambda = 0.43, $F_{2,34} = 22.5, P < 0.001$; backward: Wilks’ Lambda = 0.43, $F_{2,34} = 22.5, P < 0.001$) with MBD and HL (both with $P < 0.001$) remaining as most significant, suggesting robust discrimination. The DFA correctly classified all

<table>
<thead>
<tr>
<th>Morphometric Character</th>
<th>F ($n = 7$)</th>
<th>M ($n = 30$)</th>
<th>t-value</th>
<th>Partial $\eta^2$</th>
<th>$P$</th>
<th>% Dimorphism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head length (HL)</td>
<td>67.3 ± 0.4</td>
<td>70.5 ± 0.3</td>
<td>4.31</td>
<td>0.35</td>
<td>&lt;0.001</td>
<td>45.7</td>
</tr>
<tr>
<td>Minimum bill depth (MBD)</td>
<td>16.2 ± 0.1</td>
<td>18.2 ± 0.2</td>
<td>5.01</td>
<td>0.42</td>
<td>&lt;0.0001</td>
<td>10.9</td>
</tr>
<tr>
<td>Bill length (BL)</td>
<td>49.3 ± 0.5</td>
<td>50.8 ± 0.4</td>
<td>1.94</td>
<td>0.06</td>
<td>0.06</td>
<td>3.1</td>
</tr>
<tr>
<td>Tarsus length (TL)</td>
<td>64.8 ± 0.6</td>
<td>65.9 ± 0.4</td>
<td>1.21</td>
<td>0.04</td>
<td>0.23</td>
<td>1.6</td>
</tr>
<tr>
<td>Middle toe length (MTL)</td>
<td>76.3 ± 0.8</td>
<td>78.0 ± 0.4</td>
<td>1.80</td>
<td>0.08</td>
<td>0.08</td>
<td>2.2</td>
</tr>
<tr>
<td>Wing length (WL)</td>
<td>63.6 ± 0.3</td>
<td>64.5 ± 0.3</td>
<td>1.53</td>
<td>0.06</td>
<td>0.14</td>
<td>1.3</td>
</tr>
<tr>
<td>Body mass (BM)</td>
<td>1,186 ± 21</td>
<td>1,260 ± 17</td>
<td>2.05</td>
<td>0.11</td>
<td>0.048</td>
<td>5.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Head length</th>
<th>Minimum bill depth</th>
<th>Bill length</th>
<th>Tarsus length</th>
<th>Middle toe length</th>
<th>Wing length</th>
<th>Body mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head length</td>
<td>0.35*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum bill depth</td>
<td>0.14</td>
<td>0.58*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bill length</td>
<td></td>
<td></td>
<td>0.24</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus length</td>
<td></td>
<td></td>
<td></td>
<td>0.32</td>
<td>0.46*</td>
<td></td>
<td></td>
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<tr>
<td>Middle toe length</td>
<td></td>
<td>0.25</td>
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<td>0.21</td>
<td>0.28</td>
<td>0.47*</td>
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<tr>
<td>Wing length</td>
<td>0.36*</td>
<td>0.31</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.34*</td>
</tr>
<tr>
<td>Body mass</td>
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* P < 0.05.

We recorded a slight male bias, based on molecular markers, in our sampling effort. This may be due to time of year (establishment and...
defense of territories) when morphometric characteristics were measured. A similar pattern of a putative male-biased sex ratio was reported by others at the same stage of the breeding cycle (Marchant and Higgins 1990). The strong statistical significance of the discriminant functions, the consistency of the three DFAs in selection of discriminating variables (MBL and HL), and the high proportion (95%) of individuals that were correctly classified, despite the relatively low number of females, suggests our results represent a real biological pattern. We acknowledge our findings could be biased if different-sized males and females returned to the colony at different times of the breeding cycle (e.g., smaller females visited the colony earlier than did larger individuals). However, we know of no evidence suggesting such a pattern.

We detected clear morphometric differences between females and males. On average, the body mass of males was 6% larger than females; male procellariiform seabirds are commonly larger than females (Brooke 2004). Our DFAs demonstrated characteristics of the head and bill (HL and MBD) were the best discriminators of gender, a finding reported in other studies of procellariids (Genovart et al. 2003, Guitting et al. 2004, O'Dwyer et al. 2006, Bourgeois et al. 2007, Thalmann et al. 2007, Navarro et al. 2009). Bill sizes of the Westland Petrel were consistently strong predictors for classifying gender, in parallel with the statistically similar findings reported in prior work using DFA in two congeners, White-chinned Petrel (P. aequinotialis) and Grey Petrel (P. cinerea) (Brooke 1986, Ryan 1999).

Differences in morphometric characteristics may have consequences for how females and males vary in foraging behavior (Kato et al. 2000, Phillips et al. 2004). This may be particularly true for differences in head and bill characteristics. For example, the larger bill of male Southern Giant Petrels (Macronectes giganteus) may make them more efficient than females when competing for access to carcasses (González-Solís and Croxall 2005). We found distinct differences in head and bill characteristics between female and male Westland Petrels; however, at present it is unclear whether females and males forage differently. These morphological differences also may be due to sexual selection and/or reproductive role division, potentially serving as an honest signal for mate attraction and/or maintenance and defense of nest sites (Hedrick and Temeles 1989, Navarro et al. 2009).

Our study is the first to develop and use DFA to discriminate female and male Westland Petrels. We suggest the canonical discriminant and classification functions we derived he validated with additional samples. We also recommend that morphometric measurements be taken during different times of the breeding season and between years, as some measurements may vary over these scales (Phillips and Furness 1997). Standard molecular and histological methods for classification of gender of birds, such as DNA hybridization, Polymerase Chain Reaction (PCR), and cloacal examination, while preferred, also have several limitations (Daniel et al. 2007). For example, use of molecular techniques may not be practical in the field when knowledge of gender of study subjects is immediately required. Similarly, accuracy of cloacal examination may be limited outside of the incubation phase (O’Dwyer et al. 2006). Our study shows promise in use of select morphometric characteristics for predicting gender of Westland Petrels under field conditions.

ACKNOWLEDGMENTS

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SIZE DIMORPHISM, JUVENAL PLUMAGE, AND TIMING OF BREEDING OF THE HYACINTH VISORBEARER (AUGASTES SCUTATUS)

LICLEIA DA CRUZ RODRIGUES1,2 AND MARCOS RODRIGUES1

ABSTRACT.—The Hyacinth Visorbearer (Augastes scutatus) is a poorly known hummingbird endemic to the Cadca do Espinhaço in southeastern Brazil and is classified as near threatened with global extinction. We verified size dimorphism of males and females, describe the plumage patterns of juveniles, and detail the reproductive period of this species in Serra Cipó National Park within the municipality of Morro do Pilar in the State of Minas Gerais, Brazil during August 2007 to July 2009. Adult males were significantly larger than adult females in all measurements assessed. Variables that best differentiate males and females are body mass, total body length, occipital width, bill length, and wing chord. We demonstrated that it may be possible to assign gender of the majority of young of this species, based primarily on the color of the side of the neck and the tract of feathers that circles the visor. There is some indication of a greater concentration of reproductive effort during the dry season, when more juveniles and active nests were recorded. However, we captured fledged young in January, February, and March supporting a breeding period throughout the year for the Hyacinth Visorbearer. This suggests rainfall in the region is the most influential factor in timing of breeding of this species. Received 19 February 2011. Accepted 28 June 2011.

The Hyacinth Visorbearer (Augastes scutatus) is endemic to the Cadca do Espinhaço in southeastern Brazil with a distribution restricted to the south-central portion of the highlands. The species occurs only at altitudes >1,000 m along the southern part of the range (Iron Quadrangle = Quadrilátero Ferrífero) in the Serra do Cipó to the Serra do Pau D'Arco in northern Minas Gerais, almost to the southern border of Bahia (Vasconcelos 2008). The Hyacinth Visorbearer appears to be sensitive to changes in habitat, as it has not been observed in disturbed areas of the Cadca do Espinhaço (Vasconcelos 1999). The species' habitat is primarily threatened by destruction of large tracts of rocky fields locally known as canga (rocky outcrops that are rich in iron oxide) for extraction of iron (Jacobi and Carmo 2008). Mining activity in these canga areas probably led to the local extinction of Hyacinth Visorbearer in certain localities of the Iron Quadrangle (Vasconcelos 1999, Vasconcelos and Rodrigues 2010). This species has a highly restricted geographical distribution and occurs in habitat that is subject to significant anthropogenic pressures. Thus, the Hyacinth Visorbearer has been classified as near threatened with global extinction (BirdLife International 2010).

The Hyacinth Visorbearer is considered sexually dimorphic, as males are distinguishable from females by their more intensely iridescent blue-green forehead, chin and throat, and the presence of a narrow black band around the visor, except on the lower part of the throat. The collar is white or pale pink and the sides of the neck, chest, and abdomen are iridescent blue and/or violet, varying by individual (Fig. 1A). The forehead, chin, and throat of females usually have a slight infusion of gold coloration, while the feather tract that surrounds the visor is dark brown and the sides of the neck are blue; there is an infusion of paris green and some isolated yellow and violet feathers in some individuals. The chest and abdomen are predominantly paris green with some specimens having isolated feathers in this region that are more brown, blackish-gray and blue (Fig. 1C) (Abreu 2006). The intensity of polymorphism of the Hyacinth Visorbearer (Abreu 2006), led to description of two subspecies: Augastes scutatus soaresii (Ruschi 1962) and A. scutatus iset (Grantsau 1988). However, Abreu (2006) demonstrated that A. scutatus can not be fragmented into other taxa and that these subspecies should be considered invalid.

Morphometric data are available only for a small number of specimens (Abreu 2006). Size dimorphism between males and females was previously unknown and both juvenile males and females look like adult females (Abreu 2006). They differ slightly in the coloration of the throat, chest, and abdomen, which is mostly varying shades of brown or gray that are gradually
replaced by feathers with the characteristic adult coloration as the individual age classes. Field observations indicate it is possible to differentiate fledgling juvenile males and females.

Little is known about the life history of this endemic hummingbird despite the importance of the reproductive period of a particular species being fundamental to establishment of conservation and management programs. There are records of active nests with two eggs in January (Ruschi 1962), females building nests in July (Grantsau 1988), two active nests in June and July (Vasconcelos et al. 2001), and another nest discovered in July that was active in August and September (Costa and Rodrigues 2007). Thus, it remains unclear whether there is a well-defined reproductive period in this species.

Our objectives were to: (1) ascertain whether or not there is significant size dimorphism between adult male and female Hyacinth Visorbearers, (2) describe the plumage patterns of juveniles, and (3) document the reproductive period of this species.
in the campos rupestres (rocky fields) habitat in
the Alto do Palácio, Region of Serra do Cipó National Park in southeastern Brazil.

METHODS

Study Area.—The study was conducted in the Alto do Palácio (AP) (19° 15' S, 43° 31' W) in the
northern part of Serra do Cipó National Park (SCNP) and comprises the southern portion of the
Cadeia do Espinhaço (Rodrigues et al. 2005). The study area is within the municipality of Morro do
Pilar, State of Minas Gerais, in southeastern Brazil.

The AP region is in the eastern portion of Serra
do Cipó and is characterized by wet campos
rupestres habitat and a strong influence of certain
vegetation that is typical of the Atlantic Forest
biome. The landscape is a mosaic of: (1) typical
campos rupestres, which are areas of rocky
outcrops with herbaceous vegetation and shrubs
including Bromeliaceae, Cactaceae, Velloziaceae,
Orchidaceae, Asteraceae, and scattered trees up to
3 m in height, especially Eremanthus erythropappus; (2) open fields, composed predominantly of
herbaceous species of Cyperaceae, Poaceae, and
Eriocaulaceae, and small shrubs with an average
height of 1 m; and (3) capões de mata, which are
small areas of dense forest-like vegetation asso-
ciated with wetter areas, such as springs and small
streams with trees up to 8 m in height and many
epiphytic plants. Representatives of the Melasto-
mataceae and Asteraceae, principally Miconia
chartacea and Eremanthus cronomoides, respec-
tively, typically dominate the edges of these
capões de mata.

The AP region experiences extreme variation in
rainfall with wet summers (mainly from Nov to
Jan) and dry winters (mainly from Jun to Sep)
(Madeira and Fernandes 1999). There is, usually,
a soil water deficit from May to August, which
coincides with the coldest months of the year,
while there is excess soil water from November to
March, the warmest months of the year (Rodri-

Data Collection.—Data were collected from
August 2007 to July 2009 with the exception of
December 2008. Ten mist nets (12 × 2.6 m, 25-
mm mesh) were used in an area of 2 ha of typical
campos rupestres in the vicinity of two capões de
mata of ~0.6 ha every month for a period of
1 week in each habitat. The open fields are areas
that facilitate the perception of mist nets by birds.
The Hyacinth Visorbearer frequents this habitat
mostly during transit between the typical campos
rupestres and capões de mata but, at times, visits
blooming species in this area (L. C. Rodrigues,
pers. obs.). We chose not to conduct mist-net
sampling in the open fields. Mist nets were
opened at dawn (0600 hrs) and kept open for 6
consecutive hrs with checks for any captured birds
every 30 min. Each captured Hyacinth Visor-
bearer was banded and identified to gender and
age, and taking standardized morphometric mea-
surements by the same person with the aid of a
manual caliper of 0.05 mm precision. Measurements
included body mass, total length, bill
length, wing chord, tail length, tarsus length,
and occipital width. Individuals were classified as
juveniles or adults based on plumage patterns.
Young males have some blue feathers on the sides
of the neck and the throat (Fig. 1B), while these
feathers in females are more yellowish-green
(Fig. 1C). Monthly searches for active nests of
the Hyacinth Visorbearer were conducted in areas
where mist nests were set, and occasionally in
other areas of the AP.

Statistical Analysis.—A D’Agostino test was
performed to examine the normality of data. A
t-test was used to assess whether or not the capture
rate of adults and juveniles differed between the
dry and rainy seasons. A t-test was performed to
examine whether or not adult males and females,
as well as juvenile males and females, differ in
body mass, wing length, tail length, tarsus length,
occipital width, total length, and bill length. The
highest and lowest values of each morphometric
measurement were excluded from analysis (Get-
was used to conduct t-tests. We used a principal
component analysis (PCA) to reduce the number
of variables under consideration. The PCA was
also used to examine which variables had the
highest loadings in the linear combination of the
first principal component (PC 1 and 2). A
discriminant analysis was performed to evaluate
our ability to correctly classify adults by gender.
The PCA and discriminant analyses were con-
ducted using Program PAST, Version 2.00
(Hammer et al. 2001).

RESULTS

Morphometrics.—Juvenile and adult females
did not differ in any morphometric measurements
that were analyzed, while juvenile males had
shorter bill length (P = 0.004, t = 2.6, n = 66),
narrower occipital width (P = 0.04, t = 2.1, n =
TABLE 1. Morphometric measurements (body mass, total length, wing chord, tail length, tarsus length, occipital width, and bill length) of adult and juvenile, and male and female Hyacinth Visorbearers in the Alto do Palácio, Brazil.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Adults</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Juveniles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass (g)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>3.5 ± 0.2</td>
<td>3.4 ± 0.3</td>
<td>2.3 ± 0.23</td>
<td>3.2 ± 0.3</td>
</tr>
<tr>
<td>Range</td>
<td>3-4</td>
<td>3-3.9</td>
<td>2.7-3.8</td>
<td>2.8-3.8</td>
</tr>
<tr>
<td>n</td>
<td>42</td>
<td>23</td>
<td>28</td>
<td>8</td>
</tr>
<tr>
<td>Total length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>89.4 ± 4</td>
<td>86.5 ± 7.4</td>
<td>87.3 ± 3.2</td>
<td>87.3 ± 3.2</td>
</tr>
<tr>
<td>Range</td>
<td>81-99</td>
<td>77-95</td>
<td>80-97</td>
<td>80-94</td>
</tr>
<tr>
<td>n</td>
<td>43</td>
<td>22</td>
<td>27</td>
<td>8</td>
</tr>
<tr>
<td>Wing chord (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>52.6 ± 2.9</td>
<td>52.2 ± 2.23</td>
<td>51.1 ± 2.4</td>
<td>50.2 ± 3.2</td>
</tr>
<tr>
<td>Range</td>
<td>46-56</td>
<td>48-55</td>
<td>46-56</td>
<td>44-53</td>
</tr>
<tr>
<td>n</td>
<td>44</td>
<td>23</td>
<td>27</td>
<td>8</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>34 ± 2.1</td>
<td>34.1 ± 2.1</td>
<td>32.2 ± 2.4</td>
<td>33.8 ± 2.8</td>
</tr>
<tr>
<td>Range</td>
<td>30-38</td>
<td>31-39</td>
<td>29.2-37</td>
<td>29-38</td>
</tr>
<tr>
<td>n</td>
<td>43</td>
<td>21</td>
<td>27</td>
<td>8</td>
</tr>
<tr>
<td>Occipital width (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>30.8 ± 0.8</td>
<td>30.3 ± 0.7</td>
<td>29.1 ± 0.9</td>
<td>29.1 ± 0.9</td>
</tr>
<tr>
<td>Range</td>
<td>29.5-33</td>
<td>28.8-31.4</td>
<td>27-30.5</td>
<td>27.6-30.5</td>
</tr>
<tr>
<td>n</td>
<td>21</td>
<td>17</td>
<td>20</td>
<td>8</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>4.6 ± 0.6</td>
<td>4.4 ± 0.7</td>
<td>4.3 ± 0.5</td>
<td>4.3 ± 0.4</td>
</tr>
<tr>
<td>Range</td>
<td>3.6-5.5</td>
<td>3.6-5.4</td>
<td>3.2-5</td>
<td>3.2-4.3</td>
</tr>
<tr>
<td>n</td>
<td>33</td>
<td>20</td>
<td>23</td>
<td>8</td>
</tr>
<tr>
<td>Bill length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>18.5 ± 1.6</td>
<td>17.5 ± 1.6</td>
<td>17.2 ± 0.7</td>
<td>17.3 ± 0.7</td>
</tr>
<tr>
<td>Range</td>
<td>16-22</td>
<td>11.9-18.9</td>
<td>15.8-18.6</td>
<td>16.4-19.2</td>
</tr>
<tr>
<td>n</td>
<td>44</td>
<td>22</td>
<td>27</td>
<td>8</td>
</tr>
</tbody>
</table>

44), and shorter overall body length ($P = 0.04, t = 1.7, n = 65$) than adult males (Table 1). The wing chord of juvenile males was longer than for juvenile females ($P = 0.03, t = -1.88, n = 33$), as was the occipital width ($P = 0.002, t = -3.12, n = 26$). Adult males had longer wing chord ($P = 0.02, t = -2.98, n = 71$), tarsus length ($P = 0.04, t = -2.3, n = 54$), tail length ($P = 0.012, t = -2.6, n = 70$), bill length ($P = 0.007, t = -4.5, n = 71$), occipital width ($P < 0.001, t = -2.6, n = 47$), total length ($P = 0.025, t = -2.4, n = 70$), and greater body mass ($P < 0.001, t = -5.5, n = 68$) than females (Table 1).

All variables included in the PCA were positively correlated with PC I with body mass, wing length, and total length variables having greater weight (Table 2). Individuals with higher scores on PC I tended to be larger with greater total length, body mass, bill length, wing chord, and occipital width. PC II described the differences in tarsus and tail lengths. Individual with higher scores on PC II had shorter wing chord and greater tarsus length. The first two principal components of the PCA (PC I and II) explained almost 60% of the variation in the total sample (Table 2). The plot of the scores for PC I and II indicate a strong difference between males and females (Fig. 2). The discriminant analysis correctly classified 92.4% of subjects (91.3% of females and 93.3% of males).

Description of Juvenile Plumage.—Thirty-four juvenile Hyacinth Visorbearers were captured. Besides coloration, juveniles were molting feathers along the whole body. It was not possible to assign gender to three captured individuals, which were predominantly gray on the throat, chest, and...
TABLE 2. Weight of morphological variables for Hyacinth Visorbearers captured in the Alto do Palácio, Brazil for the principal components (PC I, II, III, IV, V, VI, and VII) from the PCA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC I</th>
<th>PC II</th>
<th>PC III</th>
<th>PC IV</th>
<th>PC V</th>
<th>PC VI</th>
<th>PC VII</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>0.757</td>
<td>0.298</td>
<td>0.071</td>
<td>0.082</td>
<td>-0.397</td>
<td>-0.099</td>
<td>-0.397</td>
</tr>
<tr>
<td>Total length</td>
<td>0.707</td>
<td>-0.157</td>
<td>0.007</td>
<td>-0.325</td>
<td>0.560</td>
<td>-0.119</td>
<td>-0.291</td>
</tr>
<tr>
<td>Occipital width</td>
<td>0.691</td>
<td>-0.100</td>
<td>-0.448</td>
<td>0.424</td>
<td>0.036</td>
<td>-0.295</td>
<td>0.203</td>
</tr>
<tr>
<td>Bill length</td>
<td>0.681</td>
<td>-0.012</td>
<td>-0.357</td>
<td>-0.508</td>
<td>-0.253</td>
<td>0.222</td>
<td>0.188</td>
</tr>
<tr>
<td>Wing chord</td>
<td>0.655</td>
<td>0.103</td>
<td>0.673</td>
<td>-0.040</td>
<td>-0.053</td>
<td>-0.117</td>
<td>0.296</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.522</td>
<td>-0.659</td>
<td>0.135</td>
<td>0.344</td>
<td>0.017</td>
<td>0.387</td>
<td>-0.062</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>0.289</td>
<td>0.832</td>
<td>-0.059</td>
<td>0.230</td>
<td>0.269</td>
<td>0.302</td>
<td>0.045</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>2.803</td>
<td>1.123</td>
<td>0.809</td>
<td>0.725</td>
<td>0.613</td>
<td>0.415</td>
<td>0.389</td>
</tr>
<tr>
<td>Percentage of variation</td>
<td>40.05</td>
<td>18.051</td>
<td>11.55</td>
<td>10.359</td>
<td>8.760</td>
<td>5.940</td>
<td>5.272</td>
</tr>
</tbody>
</table>

abdomen, had some slight red coloration at the base of the bill, a brownish forehead and brown chin, and a white spot between the eye and the throat (Fig. 1E). These are possibly the youngest juveniles captured and had recently fledged.

Juvenile males had some blue feathers on the neck, chest, and abdomen and, at times, had pale pink feathers on the collar and the tract of feathers that outlines the visor, which is typically dark gray (Fig. 1B). Juvenile females differed from juvenile males mainly in having yellowish-green to green feathers on the throat, the tract of feathers surrounding the visor being gray or light brown, and in having fewer blue feathers on the abdomen (Fig. 1D). Some juvenile males and females also had slight red coloration at the base of the bill similar to the three juveniles that were considered to be of indeterminate gender.

Two juvenile males were recaptured one month after initial capture and still retained the typical juvenile plumage, although the gender of one had been considered indeterminate at time of first capture. Two males and one female that had gender specific juvenile plumage upon first capture, presented typical adult plumage upon recapture 1 month later.

Reproductive Period.—Adults (n = 73) and juveniles (n = 34) were captured during all
There were no significant differences in capture rate of adults between dry and rainy seasons \((P = 0.392, t = -0.8, n = 23)\), while most juveniles \((70.5\%)\) were captured in the dry season \((P = 0.001, t = -3.9, n = 23)\).

Three nests of the Hyacinth Visorbearer were recorded in the area of typical *campos rupestres* within AP. One nest was active between 22 June and 22 July 2007, one nest was not active on 24 June 2008 and was found after it was active, and the third nest was active during 19 and 21 April 2009. Both active nests had two nestlings. All three nests were constructed primarily of *Pilosocereus aurisetus* (Cactaceae), a trichome species that is endemic to Serra do Cipó, and decorated with moss.

**DISCUSSION**

Male and female Hyacinth Visorbearers were notably different in plumage and morphometric measurements. Adult males were consistently
larger than females in all measurements considered. Measurements most useful in differentiating adult males and females were body mass, total length, occipital width, bill length, and wing chord. These measurements may be used to decrease handling time in future field work. Generally, male hummingbirds tend to be larger than females (Grantsau 1988, Johnsgard 1997), and it is not surprising that Hyacinth Visorbearers were consistent with this pattern. The measurements of bill length, wing chord, and tail length documented by Abreu (2006), the only morphometric variables for which means and ranges were available for males and females, are also consistent with our findings (i.e., that males are larger than females).

Abreu (2006) noted small differences in means and ranges for certain variables, including body mass, wing chord, and tail and bill length. The ranges of Abreu’s (2006) measurements were narrower than those in our study. It is likely these differences are due to the greater number of individuals we measured. The total length of males was the only measurement taken by Abreu (2006) that had a higher mean (98.2 mm) and greater range (81–108 mm). The number of individuals (n = 14) measured by Abreu (2006) was small and possibly not viable for comparisons. These individuals were also captured at different locations along the Cadeia do Espinhaço, suggesting this particular measurement may vary to a greater extent than other morphometric measurements between different populations of Hyacinth Visorbearer.

The feather coloration pattern of juvenile male Hyacinth Visorbearers observed in our study is consistent with the description of blue on the neck noted by Schuchmann (1999) and Abreu (2006). However, previous studies have not fully described the plumage coloration and patterns of juvenile male and female Hyacinth Visorbearers. Our study suggests it is possible to accurately assign gender of the majority of juvenile Hyacinth Visorbearers based mainly on coloration of the side of the neck and the tract of feathers that circles the visor. It is common to find different plumage patterns between juvenile male and female hummingbirds that exhibit strong sexual dimorphism (Newell et al. 2007, Juina et al. 2010). This may offer a simple and important tool for population studies that estimate sex ratios among juveniles. Our data also suggest that individual Hyacinth Visorbearers retain some juvenile plumage for at least 2 months.

There is some indication of a greater concentration of reproductive effort during the dry season, when more juveniles and active nests were recorded. However, captured fledged young in January, February, and March support a breeding period for the Hyacinth Visorbearer of throughout the year. Further evidence is necessary to confirm this hypothesis. The reproductive period of tropical hummingbirds is usually synchronized with peaks in flowering of particular plant species during the dry or rainy season (Skutch 1950, Sílves 1980, Schondube et al. 2003), which seems to be directly associated with preference of certain hummingbird species for specific blooming plants. Some species of hummingbirds, however, are known to breed throughout the year (Johnsgard 1997).

The abundance of flowers in AP that Hyacinth Visorbearer are known to visit was constant throughout the year; the highest density of non-ornithophilous flowers was registered at the end of the rainy season and early dry season (Rodrigues 2011), which coincides with the increase of young of this species. The consistent availability of preferred resources may favor the capacity of this hummingbird to reproduce throughout the year. However, there is nearly constant rainfall in the region from November to February. There are certain periods, particularly during December and January, when there is constant rainfall for as many as 10 consecutive days or more (L. C. Rodrigues, pers. obs.). Rainfall can have a direct influence on concentration of nectar (Aizen 2003), which consequently can cause the birds to avoid expending energy on acquiring highly diluted nectar (Rocca-de-Andrade 2006), which has a much lower energetic value. Moreover, nests of Hyacinth Visorbearers were recorded in small shrubs and exposed to direct sunlight and rain. Thus, it may be more advantageous for Hyacinth Visorbearers to reproduce during the dry season when risk of damage to nests, as well as nectar dilution, is less and the energetic value of available resources is likely to be much higher.

Further work on this species should examine whether or not the Hyacinth Visorbearer has one or more reproductive periods per year and if the parapatric species, Hooded Visorbearer (Augastes lamachella), exhibits similar juvenile plumage patterns. Ultimately, more comprehensive and long-term life history studies of this and other possible threatened and endangered species in southeastern Brazil and elsewhere are needed for effective conservation planning.
ACKNOWLEDGMENTS

We thank M. L. M. Varela, D. F. Dias, F. C. Diniz, and Renato Rocha for help during field work, and the Chico Mendes Institute (ICMBio) and Directors of Serra do Cipó National Park for logistical support. We are grateful to CNPq for a Ph.D. scholarship awarded to LCR. MR thanks CNPq for financial assistance through the research productivity and support award (473428/2004-0 and 300731/2006-0), as well as FAPEMIG (PPM APQ-0434-5.03/07) and the Fundação O Boticário de Proteção a Natureza for additional financial support. We thank M. F. Vasconcelos, A. C. Araujo, J. B. Harris, and C. E. Braun for valuable suggestions on the manuscript.

LITERATURE CITED

MORPHOMETRIC VARIATION AND POPULATION RELATIONSHIPS OF KRÜPER’S NUTHATCH (SITTA KRUEPERI) IN TURKEY

TAMER ALBAYRAK,1,4 AURELIEN BESNARD,2 AND ALI ERDOĞAN3

ABSTRACT.—We studied the population relationships of Krüper’s Nuthatch (Sitta krueperi) by capturing 12 individuals using mist nets in six different areas in Turkey during the breeding season, from March to June 2005-2008. Forty-one different morphometric characters were measured. Morphometric characters measured (X ± SD) were: body mass = 13.11 ± 0.88 g, wing length = 74.79 ± 2.35 mm, bill length = 17.65 ± 0.76 mm, and tarsus length = 19.10 ± 0.93 mm, respectively. A stepwise discriminant analysis of four populations retained seven statistically significant measurements: body mass, wing length, length of P 8, alula, bill height, back nail, and left nail. These analyses allowed discrimination among populations. The population in the Aladaglar Mountains differed from others even though it overlapped with the population in the Lütfi Biiyiik Yıldırım Research Forest, and marginally with the population at Kartalkaya Mountain. Cross validation for the other three populations confirmed large overlap in morphometric characteristics although the population at the Lütfi Biiyiik Yıldırım Research Forest seemed to be intermediate between populations at Aladaglar Mountains and in the Kazdağlar Mountain-Kartalkaya Mountain complex. Received 12 February 2011. Accepted 12 June 2011.

The Anatolian Peninsula of Turkey exhibits important biodiversity due to high climatic diversity, topographic variation, and habitat fragmentation. Anatolia is considered to be one of the most important refugia in southern Eurasia during glacial periods (Ciplak 2004). The distribution of sensitive species changed during both the Pliocene and Pleistocene, and contracted during the following interglacial period due to changes in climate (Ciplak 2004). Successive retreats and expansions of glacial ice may have resulted in complex genetic structuring of species isolated in multiple refugia and by postglacial colonization (Howes et al. 2006). Forest vegetation may have survived in several Quaternary glacial refugia in the northern and southern parts of the Anatolian Peninsula (Hughes et al. 2006). Anatolia exhibits substantial altitudinal variation ranging from 0 to 5,137 m asl (1,100 m asl average elevation), which resulted in extensive habitat fragmentation. This topographic relief had an important role in Pleistocene changes by constraining distribution corridors for latitudinal dispersal and providing suitable habitats during altitudinal shifts (Ciplak 2008). Anatolian forests are mainly composed of fragmented areas of Pinus spp., Abies spp., Cedrus spp., and Picea spp. (Akman 1995, Albayrak et al. 2010).

Krüper’s Nuthatch (Sitta krueperi) is an endemic species strictly confined to coniferous forests (Löhrl 1988, Cramp and Perrins 1993, Harrap and Quinn 1996, Hagemeijer and Blair 1997, Matthysen 1998, Albayrak and Erdogan 2005a) whose range is mainly restricted to Anatolia, Lesvos Island, and the Caucasian region (BirdLife International 2004; Albayrak and Erdogan 2005a, b; Albayrak et al. 2006). Krüper’s Nuthatch populations, like those of many forest bird species, have been declining in Turkey and Lesvos Island (BirdLife International 2004). The species is categorized as a species of European conservation concern, SPEC 2 by BirdLife International (2004), and near threatened by the IUCN (2010). It is mostly sedentary with limited post-breeding dispersal and seasonal altitudinal movements (Cramp and Perrins 1993, Harrap and Quinn 1996, Handrinos and Akriotis 1997).

We hypothesized this species would be expected to have isolated populations. Our objectives were to: (1) explore potential population diversity and characteristics at the morphometric level in Anatolia, and (2) characterize the little known morphometry of the species.

METHODS

Study Site.—We selected six different areas (Fig. 1) locally occupied by Krüper’s Nuthatch in Turkey: Aladaglar Mountains (ALA, 930 m asl; red pine [Pinus brutia] forest), Alanya (ALY, 1,300 m asl; red pine forest), Lütfi Biiyiik Yıldırım Research Forest (BUK, 650 m asl; red...
FIG. 1. Study sites in the Anatolian Peninsula, Turkey and significant differentiation of Krüper’s Nuthatch populations. World distribution is in gray.

Bird Census.—Surveys for nuthatches were conducted during the breeding season between March and June 2005–2008 to understand possible gender differences (breeding females can be identified from brood patches). In total, 78 m (2 × 12, 2 × 10, 2 × 8, and 3 × 6 m) of mist nets were set and playback of calls was used to attract nuthatches; 82 individuals were captured. Only males were expected to be attracted by playback of calls but five individuals captured had brood patches and were probably females. It is not possible to separate most adult males from adult females based on plumage characteristics although there is limited information in the literature (Cramp and Perrins 1993). These five individuals were excluded from the population comparison analysis since they may differ from males and were too few to be analyzed separately.

Forty-one different morphometric characters based on Svensson (1992) were measured by the same observer (TA) in all populations: body mass, wing length, tail length, bill length (BL), bill width at nostril (BW), bill height at nostril (BH), length of bill apex to head back (LBAHb), length of nostril to bill apex (LNBA), length of black on forehead (LBf), alula, tarsus, four nails of left foot, all 10 primaries and nine secondaries of the left wing, and all six rectrices from the left side. Digital calipers and a digital balance were used for taking measurements. All individuals were released after measurement at their capture location.

Data Analyses.—We performed a stepwise discriminant analysis to explore the level of morphologic differentiation among Krüper’s Nuthatch populations. We retained only 15 characters subjectively supposed to be the most discriminating among populations, and for which sufficient individuals were measured. Populations ALY and ADR had few individuals with complete mea-
TABLE 1. Descriptive statistics of morphometrics of Krüper's Nuthatch, Anatolian Peninsula, Turkey.

<table>
<thead>
<tr>
<th>Character</th>
<th>n</th>
<th>Mean ± SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass, g</td>
<td>72</td>
<td>13.11 ± 0.88</td>
<td>11.17</td>
<td>14.80</td>
</tr>
<tr>
<td>Wing, mm</td>
<td>77</td>
<td>74.79 ± 2.35</td>
<td>65.32</td>
<td>80.00</td>
</tr>
<tr>
<td>Tail, mm</td>
<td>75</td>
<td>37.45 ± 2.06</td>
<td>31.04</td>
<td>42.00</td>
</tr>
<tr>
<td>BL, mm</td>
<td>77</td>
<td>17.65 ± 0.76</td>
<td>15.47</td>
<td>19.23</td>
</tr>
<tr>
<td>BW, mm</td>
<td>76</td>
<td>4.55 ± 0.34</td>
<td>3.78</td>
<td>5.51</td>
</tr>
<tr>
<td>BH, mm</td>
<td>76</td>
<td>3.87 ± 0.24</td>
<td>3.32</td>
<td>4.68</td>
</tr>
<tr>
<td>LBaHb, mm</td>
<td>66</td>
<td>36.18 ± 0.90</td>
<td>34.09</td>
<td>38.36</td>
</tr>
<tr>
<td>LNBr, mm</td>
<td>77</td>
<td>12.64 ± 0.68</td>
<td>11.14</td>
<td>14.87</td>
</tr>
<tr>
<td>Alula, mm</td>
<td>66</td>
<td>18.55 ± 1.22</td>
<td>13.62</td>
<td>22.00</td>
</tr>
<tr>
<td>Tarsus, mm</td>
<td>76</td>
<td>19.10 ± 0.93</td>
<td>16.59</td>
<td>24.50</td>
</tr>
<tr>
<td>Back nail, mm</td>
<td>70</td>
<td>6.50 ± 0.34</td>
<td>5.56</td>
<td>7.34</td>
</tr>
<tr>
<td>Left nail, mm</td>
<td>62</td>
<td>4.04 ± 0.36</td>
<td>3.46</td>
<td>4.93</td>
</tr>
<tr>
<td>Mid. nail, mm</td>
<td>63</td>
<td>4.63 ± 0.39</td>
<td>3.95</td>
<td>6.36</td>
</tr>
<tr>
<td>Inner nail, mm</td>
<td>63</td>
<td>3.78 ± 0.36</td>
<td>3.10</td>
<td>4.71</td>
</tr>
<tr>
<td>LbF, mm</td>
<td>58</td>
<td>14.25 ± 1.98</td>
<td>9.86</td>
<td>19.66</td>
</tr>
</tbody>
</table>

measurement data, and were excluded from the analysis. The discriminant analysis was performed on four populations totaling 60 individuals.

Our data set indiscriminately incorporated adult males and females, and possibly some juveniles; we suspected that size could be a confusing factor in the discriminant analysis. We thus focused on shape analysis (morphology instead of morphometry) to remove the potential effect of size and avoid misinterpretation of the results. Size differences were removed using a bicentering transformation on the log of the measurements. Two individuals in this transformation were linked by a multiplying constant and became identical (Gower 1976). This approach is classically used to study morphology instead of morphometry (Yoccoz 1993). Bicentering was performed using the library Ade4 (function bicenter.wt) (Chessel et al. 2004) and R 2.10.1 (R Development Core Team 2009).

The data set was subjected to stepwise discriminant analysis to ascertain which morphological traits best discriminated among the four populations. All traits that remained in the model when the stepwise selection process stopped were significantly discriminating among populations. The stepwise discriminant analysis was performed using SAS/STAT® software (PROC STEPDISC) (SAS 1985). PROC DISCRIM (SAS 1985) was used to obtain the discriminant function. The function was validated by a leave-one-out cross validation procedure. The leave-one-out cross-validation procedure in discriminant analysis consists of recalculating the discriminant function several times, based on all birds except the one which is classified using the estimated function. Each classified bird in this procedure was allocated to the group with the nearest centroid, and the proportion of correctly allocated individuals was calculated (Ripley 1996). A graphical representation of the classification was also obtained using library Ade4 in R 2.10.1 (R Development Core Team 2009).

RESULTS

Morphometric Characterization.—We found a small statistically significant differentiation between individuals without a brood patch and with a brood patch for bill length, bill width, and $P_7$ (t-test; $P < 0.05$). We recorded no measurements for brood patch individuals due to the low sample size ($n = 5$, probably females). Mean ($±$ SD), range, and sample size for the 15 morphometric measurements used in the discriminant analysis (Table 1), and measurements of primaries, secondaries, and tail feathers varied (Table 2). The longest primary was $P_6$ and longest secondary was $S_2$ (Table 2).

Population Relationships.—The stepwise discriminant analysis retained only seven measurements allowing discrimination among populations based on body mass, wing length, length of $P_6$, alula, BH, back nail, and left nail (Table 3). The plot of the first two canonical variables indicates small differences among populations as the overlaps are great (Fig. 2). The discriminant analysis correctly classified 50 of the 60 birds, i.e., 83% (Table 4). However, the cross validation...
procedure correctly classified only 30 birds, i.e., 50% (Table 4), which is low. The ALA population is quite different from the others even though it overlaps with population BUK and marginally with population KAR. Cross validation confirmed these results by correctly assigning 75% of the birds. Cross validation of the three other populations confirmed the large overlap in morphological characteristics, although population BUK was intermediate between population ALA and the KAZ-KAR complex.

DISCUSSION

The morphometric characteristics of Krüper’s Nuthatch are poorly known. Only measurements of wing length, tail length, bill length, tarsus, and body mass, which are similar to our results, have been recorded from small numbers of individuals (Cramp and Perrins 1993, Roselaar 1995, Harrap and Quinn 1996). Differentiation among Krüper’s Nuthatches is not known although a few measurements for both males and females were given by Cramp and Perrins (1993) and Harrap and Quinn (1996). We compared measurements of morphometric characteristics among populations using males that were captured using playback of calls during the breeding season and which did not exhibit a brood patch. There was slight dimorphism in the species, and verification of the measurements of males and females now depends on molecular identification of individuals.

Geographical distance and habitat fragmentation are considerable among populations in the Anatolian Peninsula. Our results indicate there may be exchange among populations, possibly because of the existence of suitable corridors, especially between BUK and the KAR-KAZ complex. Krüper’s Nuthatch is probably capable of long distance movement and it is unlikely that only isolation by distance can produce differentiation among populations. We detected some differentiation among populations in the data set. The ALA population is quite different from the three other populations even if it overlaps with population BUK and marginally with the population in the KAR-KAZ complex.

This could be the result of the existence of both southern and northern refugia during glacial periods which were partially reconnected after isolation by distance. ALA and BUK are both in the southern refugia and overlap in morphologic characters was observed between them. The KAR-KAZ complex is localized in the northern part of Anatolia and populations are probably sufficiently close to exchange some individuals. ALA is distant from these two northern populations. These two complexes are also separated by habitat fragmentation and high mountains, which are unoccupied by the species (Fig. 1).

**TABLE 2.** Measurements (mm) of primary, secondary, and tail feathers of Krüper’s Nuthatch, Anatolian Peninsula, Turkey.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean ± SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2nd</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3rd</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4th</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>5th</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>6th</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>7th</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8th</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9th</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10th</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 3.** Stepwise discriminant analysis of morphometric characteristics of Krüper’s Nuthatch, Anatolian Peninsula, Turkey.

<table>
<thead>
<tr>
<th>Step</th>
<th>Variable</th>
<th>Wilk’s $\lambda$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Body mass</td>
<td>0.72</td>
<td>0.0003</td>
</tr>
<tr>
<td>2</td>
<td>Back nail</td>
<td>0.60</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>3</td>
<td>P 8</td>
<td>0.52</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>4</td>
<td>Wing</td>
<td>0.38</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5</td>
<td>Alula</td>
<td>0.33</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6</td>
<td>BH</td>
<td>0.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>7</td>
<td>Left nail</td>
<td>0.26</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
The BUK population is classified as intermediate between the KAR-KAZ complex and ALA. This agrees with both the refugia hypothesis of later partial reconnection and the hypothesis of isolation by distance only. The Great Reed Warbler (Acrocephalus arundinaceus) population in the Eurasian breeding range of the species has two clades that have colonized from two separated refugia in Europe and the Middle East (Hansson et al. 2008). The forest types of KAR and KAZ were black pine while the other populations occupied red pine forest. These forest types may also have affected the morphometrics independently of isolation due to long distances or refugia disconnection between locations ALA and the KAR-KAZ complex (min = 440 km; Fig. 1).

Anatolian refugia are known to have affected the evolution of structured populations in several groups including grasshoppers (Ciplak 2008), small mammals (Castiglia et al. 2009), and a passerine bird (Hansson et al. 2008). For example, the Anstrates genus of Orthoptera arose from an ancestral stock during the Pliocene era in northwestern Anatolia whose range later expanded and contracted under the effects of the ice ages (glacial and interglacial periods, respectively).
(Ciplak 2004). The explanation for the present findings regarding differentiation of nuthatch populations may be isolation of subpopulations during the glacial period and ongoing habitat fragmentation. There may have been a minimum of two different refugia, southern and northern, for Krüper’s Nuthatch during the glacial periods due to the topographic structure of Anatolia. The extent of isolation may increase with ongoing fragmentation of breeding habitats due to logging, deforestation, etc.

Our study did not fully answer the question why Krüper’s Nuthatch exhibit morphologic differentiation in Turkey. Our results agree with the already observed pattern of isolation by distance, and also the existence of northern and southern refugia during recent glacial periods. Molecular markers can provide more information about the biogeographic history of this species and can also assess the relationship among isolated subpopulations. Our results should be useful in conservation applications and future research. The population diversity of Krüper’s Nuthatch at present is small, but still detectable, and could be used to identify and design protected areas for subpopulations and help with conservation efforts.

ACKNOWLEDGMENTS

We thank Metin Balçay who provided valuable technical assistance in our field research and Figen Erkoç for valuable comments and suggestions. This study was supported by the Akdeniz University Research Fund (Nr: 2005.03.01.21.01).

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A PROBABILISTIC MODEL FOR PRESENCE OF EURASIAN NUTHATCH (SITTA EUROPAEA) IN THE ALBORZ MOUNTAINS, NORTHERN IRAN

FATEMEH BAHADORI KHOSROSHAHI,1,2 AFSHIN ALIZADEH SHABANI,1 MOHAMMAD KABOLI,1 MAHMOUD KARAMI,1 MITRA SHARIATI NAJAFABADI,1 AND YOSEFALI AHMADI-MAMAQANI1

ABSTRACT.—Hyrcanian forests in the northern Alborz Mountains contain many resident and migrant passerines, but the ecological relationships of the species are obscure. We identified the ecological factors (forest structure, type, and topography) that could explain the distribution of the Eurasian Nuthatch (Sitta europaea) and its habitat suitability in this region. Significant habitat parameters for presence-absence of Eurasian Nuthatch were height, diameter, stand, and type of trees. Our model successfully predicted the presence probability of nuthatches and that suitable habitats strongly depend on abundance of old trees, especially Oriental beech (Fagus orientalis) and European hornbeam (Carpinus betulus). These data suggest forest structure is the key factor in bird habitat use and suitability, and reveal the necessity of adaptive logging activities in Hyrcanian forests. Received 22 June 2010. Accepted 16 April 2011.

Hyrcanian forests in the northern Alborz Mountain ranges of northern Iran contain specific and distinctive habitats which support a wide variety of fauna and flora. Their vertical distributions are from sea level to 2,800 m asl. These forests have high similarity with mixed broadleaf forests in central Europe, but are more diverse and support more species (Marvi Mohajer 2005). They support a significant diversity of bird fauna despite the scant distribution of forests in northern Iran. Birds in this region are closely related to the Western Palearctic (Majnoniyan et al. 2005). The Kheyrud Forest is a part of the Hyrcanian forests and supports 50 species from 24 families of birds. Most have uniform distribution and belong to Passeriformes and Falconiformes. Many birds, especially passerines, breed and winter in this area, but the ecological relationships of the species are obscure, and management strategies remain uncertain.

Habitat suitability modeling has been demonstrated to be helpful in evaluating wildlife habitats as well as effects of management activities on habitat suitability (Austin et al. 1990, Guisan and Zimmerman 2000, Bartoszewicz et al. 2008). The predictive value of habitat models can also be used to identify potential areas for species, outside of the region where the model was originally developed (Morrison et al. 1992). General Linear Models (GLMs) are frequently used to identify the major habitat factors that explain habitat selection by a species in a certain area (Backland and Elston 1993). Habitat selection among avifauna operates through a series of behavioral decisions at several spatial scales, which explains why studying distributional patterns is difficult. Habitat selection is a hierarchical process in which individuals first select the general area in which to live. Within this area they select among the available patches for breeding sites (Morrison et al. 1992, Pribil and Pieman 1997).

The Eurasian Nuthatch (Sitta europaea) is an area-sensitive species which prefers undisturbed old growth forest patches. Our objectives were to: (1) examine habitat suitability and (2) identify factors that explain the distribution of this species in Hyrcanian forests by developing a model that could predict the presence of the species with acceptable accuracy (Matthysen 1987, Bellamy et al. 1998, González-Varo et al. 2008).

METHODS

Study Area.—The study was conducted in Kheyrud Forest (8,000 ha), an educational and research forest area, in the Caspian Hyrcanian mixed forests of the Alborz Mountains in northern Iran (Fig. 1). This area is 7 km east of Nowshahr, Mazandaran Province (36° 40' to 36° 27' N, 51° 43' to 51° 22' E), at an elevation of 80 to 2,200 m asl. The climate of the area is wet with cool winters. Annual average precipitation and temperature are 1,293.3 mm and 16.1° C, respectively (Ahmadi 2006). Dominant plant communities include Parrotia-Carpinetum, Parrotia-Buxetum, Tilio-Buxetum, Querco-Carpinetum.
Fagetum, Fageto-Carpinetum, Fagetum type, and mixed Fagetum (Marvi Mohajer 2005). Soils in the study area are dominated by Rendzina, Eutric Cambisol, Orthic Luvisols, and Eutric Regosols (Sarmadian and Jafari 2001). The Kheyrud Forest is divided into seven districts of which five >6,000 ha were surveyed.

Nuthatch Survey.—We designed eight line transects in the study area along the elevation gradient and sampling points had a minimum
distance of 300 m from each other to avoid spatial autocorrelation (Gibbons et al. 1996). Each transect was visited once during the sampling period by the same observer. The observer used the sit and wait method at each sampling point to record observed and/or heard nuthatches, lasting on average 20 min. Playback of the male call was used to confirm nuthatch absence after each point count if the species had not been detected (González-Varo et al. 2008). We sampled from 0530 until 1000 hrs and avoided windy and rainy weather. There were 78 presence plots and 20 absence plots during our sampling periods (Fig. 1).

Habitat Structure Sampling.—The habitat of nuthatches at each sampling point was described in terms of landscape features, forest structure, and vegetation profile. These variables were chosen because they were the most obvious and affected the amount of cover, shelter, nest sites, mode of locomotion, and prey availability. We postulated a priori these features were most likely to influence habitat choice by nuthatches. Thirteen structural habitat variables (Table 1) were either directly measured within an 11.3-m radius (Nuret et al. 1999, Dobkin and Rich 2000) centered at each sampling point, or calculated for each point from field measurements.

Statistical Analysis.—We first verified the main tree species gradient of the study area with Correspondence Analyses (CA) for the tree species matrix (98 × 12). We extracted the first three axes of this analysis which explained 52% of tree species variances in the study area, and used them as habitat explanatory variables for regression analysis. We selected, using an AIC criterion, the combination of environmental variables that best explained the presence/absence of nuthatches using a binary logistic regression procedure. The result was a number between 0 and 1. The closer to one, the higher the probability of species presence. Correlation matrices were first constructed for the predictor variable to avoid inclusion of highly correlated variables (Pearson’s r > 0.5) in the analysis (González-Varo et al. 2008). We verified high correlation between variables TN < 20D and TN < 25H as well as TN < 20D and S1, S3 and S1, S3 and CA1, TN < 20D and S2, TN > 25H and S2, TN < 25H and S1, and selected the first in all cases.

Goodness-of-fit tests were performed to verify how well the model described the data (Alizadeh Shabani et al. 2009) using Pearson, Deviance, and Hosmer-Lemenshow procedures. Thirty new random sites were sampled in the study area to validate the best model. A Chi-square test was used to compare predicted and observed frequency of nuthatch presence/absence. All analyses were performed with STATISTICA 6.0 (Statsoft 2001) and MINITAB Version 13.1 (Minitab 2000).

RESULTS

Best Predicted Models.—Generalized linear models were performed of nuthatch presence-
TABLE 2. Generalized linear models of the presence/absence of Eurasian Nuthatch against five environmental variables related to altitude, climate, geomorphology, and vegetation. Models were ranked in each case by AIC from best to worst fitting model, and only models with ΔAIC < 2 are listed. We included the standardized coefficients, allowing assessment of relative importance for each variable included in each model.

<table>
<thead>
<tr>
<th>Model</th>
<th>TN ≥ 25H</th>
<th>TN &lt; 20D</th>
<th>S3</th>
<th>AL</th>
<th>CA3</th>
<th>ΔAIC</th>
<th>R²</th>
<th>P level of model</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.858**</td>
<td>-0.602*</td>
<td>0</td>
<td>0</td>
<td>0.64</td>
<td>0.001</td>
<td>0.61</td>
<td>0.000</td>
</tr>
<tr>
<td>2</td>
<td>0.72**</td>
<td>-0.69*</td>
<td>1.25</td>
<td>0.54</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.731**</td>
<td>-0.616**</td>
<td>1.54</td>
<td>0.43</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0.661**</td>
<td>-0.601*</td>
<td>1.91</td>
<td>0.50</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

** P < 0.005.  
* P < 0.05.  
ns. P > 0.05.

absence against five significant (P < 0.05) variables (TN ≥ 25H, TN < 20D, S3, AL, CA3). The other variables (TN < 20D, AS, FCC, CA2) did not have a significant relationship with presence-absence of nuthatches (P > 0.05). The best predicted model (AIC 29.3, P < 0.001) included two variables (Table 2), including abundance of tall trees (TN ≥ 25H = positive effects) and abundance of young trees (TN < 20D = negative effects). TN ≥ 25H was a highly significant predictor and had a positive influence on the dependent variable in all four equivalent models. In contrast, TN < 20D influenced the dependent variable. The four best selected models were identified among all models using AIC (i.e., ΔAIC < 2) (Table 2). We tested the effect of adding the variable, understory of forest (stand level 0–10 m in height [S3] = negative effects) to the second model, forest altitude (AL = positive effects) to the third model, and third axis of CA for tree species (CA3 = positive effects) to the fourth model. These changes did not have any significant effect (Z = -0.78, P = 0.055; Z = 0.9, P = 0.08; Z = 0.3, P = 0.08, respectively). The third axes was allocated to Fagus orientalis (51%), Carpinus betulus (16%), and Acer insign (15%) in the CA analysis.

The log-likelihood of the models was calculated using G-statistic. This tests whether all coefficients associated with the model variables are equal to zero versus not being equal to zero. This value is especially useful when the P-values is >0.05. The log-likelihood of the four models (range = -9.043 to -9.379), G (range = 80-81), and P-value (all P < 0.01) were similar. Thus, there is sufficient evidence that at least one of the coefficients is different from zero, given the accepted α level is <0.05.

**Goodness-of-fit Tests.**—We performed Pearson, Deviance, and Hosmer-Lemenshow tests to verify how well the models describe the data. Our results did not have significant P-values from the Hosmer-Lemenshow test for all four selected models (Table 3), indicating our models describe
the data sets well. The Deviance and Pearson tests had large P-values, indicating there is a good fit of the data in the models.

**Model Validation.**—Thirty new random sites were sampled in the study area to validate the best model. Predicted and observed outcomes were not fitted at one of the sampled points (Table 4). Chi-square results of the compared predicted and observed frequency of nuthatches presence/absence revealed a significant value ($\chi^2 = 96.76; P < 0.001$), indicating good prediction power of the models.

**DISCUSSION**

Wildlife distribution and abundance patterns depend upon many environmental factors. Our study was a simplification of the process of habitat selection and identifying the most important factors in habitat use by nuthatches. We found sufficient evidence of a relationship between presence of species and environmental variables. A general pattern explaining the relationship between habitat and species distribution was derived from the final GLMs developed for the study area. The developed model in our study successfully predicted the probability of the presence of European Nuthatches. Our study clearly showed that specific vegetation structure was the most important determinant for this species. Eurasian Nuthatches were present and nested in some of the largest (in diameter and height) trees in the Kheyrud Forest. Large trees are more likely to provide adequate and suitable holes, which are likely to be absent or too small in small trees (Bellamy et al. 1998). This agrees with previous studies conducted in areas with similar vegetation structure (Bardin 1987, Matthysen 1987, Clark 1991, Bellamy et al. 1998, Burkhardt et al. 1998, Pagenkopf and Wesolowski 2002, González-Varo et al. 2008) and significant predictors for Eurasian Nuthatch presence. Species presence in our study area was affected by a variety of tree species, but most were Oriental beach (Fagus orientalis), chestnut-leaved oak (Quercus castaneifolia), and European hornbeam (Carpinus betulus) trees which usually have larger diameter and height. Species presence is more likely in areas where beach, hornbeam, and maple are abundant based on the third axis of CA analysis in the fourth model. Deciduous woodland with a high proportion of oak and beach trees is reported (Nilsson 1976, Matthysen 1990) to be a more suitable environment for raising and feeding nuthatch offspring.

The major plant community in the Kheyrud Forest within the 80-300 m asl range is Querco-Buxetum, which supports a variety of bird species. Carpino-Fagetum gradually changed to Fagetum type from 700-1,000 m to 1,000-1,500 m asl (Marvi Mohajer 2005). The elevation category of 700-1,000 m was dominated by the Fagetum plant community. However, because of harvest of beach trees, they were replaced by hornbeam. These two elevation bands are adjacent to each other and supported the same group of avifauna. Elevation from 300 to 700 m is dominated by Querco-Carpinetum. The community in this area was Querco in the past and, due to the harvest of Querco trees, they have been replaced by hornbeam (Marvi Mohajer 2005). The prominent communities in upland are Fagetum and Querco-Carpinetum, which have characteristics of higher altitude vegetation, allowing a special group of birds to occur in this region. Comparison of individual areas with the criteria for habitat quality strongly indicated the study area included suitable habitat for nuthatches in most areas of the forest. Overall, 80% of the entire study area was estimated to be suitable for nuthatches, and the remaining area was unsuitable, because the forest has been destroyed by human activities. Also, due to steep slopes (>70%), inappropriate plant species (in terms of size and structure) caused unsuitable habitats. Forest understory (0-10 m) increases in these areas, which is shown in the second model where the S3 variable (Stand level 0-10 m in height) has a negative coefficient, indicating a negative correlation with presence of nuthatches. We observed this effect in the down slope parts of the Kheyrud Forest (from 700 m to lower altitudes) that have been destroyed and have low tree cover (a high percentage of absent points were recorded in this region; Fig. 1). Overall, Fagus orientalis, Quercus macranthera, and

<table>
<thead>
<tr>
<th>TABLE 4. Chi-square test for 30 new random sites to compare predicted and observed frequency of occurrence of European Nuthatches.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted</td>
</tr>
<tr>
<td>-----------</td>
</tr>
<tr>
<td>Suitable</td>
</tr>
<tr>
<td>Unsuitable</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
**Carpinus orientalis** create an upper border of forests in northern Iran (Marvi Mohajer 2005) allowing appropriate habitat for nuthatches in an upland region. Beach forests have turbid air (because of moisture demand) that produces dew, one of the water resources for birds (Marvi Mohajer 2005). Water resources are among the important factors for bird species diversity (Rahbek 1995, Díaz et al. 2005) and can be effective for enhancing bird richness in the 1,500-1,800 m elevation range. The positive coefficient of the altitude variable in the third model indicates the probability of nuthatch presence increases at higher altitudes.

The most important feeding guild in our study was insectivorous bird species. Most species that belonged to this guild, such as the Red-breasted Flycatcher (*Ficedula parva*), Eurasian Nuthatch, Eurasian Golden Oriole (*Oriolus oriolus*), Common Cuckoo (*Cuculus canorus*), and Common Chiffchaff (*Phylloscopus collybita*), were seen in the entire forest. Associated species with nuthatches in the Kheyrud Forest were Common Chaffinch (*Fringilla coelebs*), Coal Tit (*Periparus ater*), Eurasian Wren (*Troglodytes troglodytes*), Song Thrush (*Turdus philomelos*), Common Blackbird (*T. merula*), European Green Woodpecker (*Picus viridis*), Syrian Woodpecker (*Dendrocopos syriacus*), and Common Pheasant (*Phasianus colchicus*). Most studies report that nuthatches nest in holes produced by woodpeckers and may overlap in habitats used. We cautiously conclude the Eurasian Nuthatch can potentially be considered as an indicator of old growth and intact Hycranian forests. Some species in Hycranian forests are of conservation concern; for example, the Common Pheasant is a protected species that live in northern forests. Pheasant habitat in the study area overlapped with habitats used by nuthatches. Thus, we can provide better habitat conditions for Common Pheasant survival in this area by maintaining nuthatch habitats in Hycranian forests.

Our model indicated habitat variables could predict the appropriate distribution of habitats. Habitat variables are good predictors of distribution, and our estimates were good approximations for the actual distribution of nuthatches. The presence of an individual does not prove the habitat is suitable for breeding based on our analysis of presence-absence data. For example, presence may have occurred because of local movements. There is not an organized sampling method for bird species in the study area which is why we repeated the sampling and obtained similar results. The model we developed indicated high probability of species occurrence and validation indicated the model was effectively functional within the study area.

**ACKNOWLEDGMENTS**

We thank the many people who helped us with field work. In particular we thank Mansour Alibadian and Vahid Etemad for critical discussion and assistance in numerous other ways. The research was conducted with the financial support of the Department of Fisheries and Environment, Faculty of Natural Resource, Tehran University, Iran.

**LITERATURE CITED**

Ahmad, T. 2006. Determination of the physical, chemical and taxonomic properties of forest soil of Namulan District of Kheyrud in relation to plant communities and also evaluation. Dissertation. Islamic Azad University, Tehran, Iran.


BREEDING ECOLOGY OF THE EMEI SHAN LIOCICHLA (LIOCICHLA OMEIENSIS)

YI-QIANG FU,1,2 SIMON D. DOWELL,3 AND ZHENG-WANG ZHANG,4

ABSTRACT.—We studied the breeding ecology of the Emei Shan Liocichla (Liocichla omeiensis) in two nature reserves (Laojunshan and Wawushan) in Sichuan, China from March to August 2009 and April to August 2010. The breeding density (mean ± SE) was between 1.20 ± 0.46 and 1.55 ± 0.56 males/km2, and the breeding season was from the April to mid-August and from mid-May to late August in Laojunshan Nature Reserve in 2009 and 2010, respectively. The species used the edges of or gaps within natural broadleaf forest between elevations of 1,450 and 2,150 m for nesting. Vegetation around nests was mainly bamboo (Chimonobambusa szechuanensis), small shrubs, and vines with few large trees. Nests were cup-shaped with a mean height of 137.5 ± 4.6 cm above the ground. Nests were mainly on C. szechuanensis. Females laid one egg per day in the morning, and the mean (± SE) clutch size was 2.9 ± 0.2 eggs. Incubation started after the last egg was laid. Both males and females were observed participating in incubation, provisioning, and brooding the nestlings. Hatching success, fledging success, and nest success were 58.6, 70.8, and 27.5%, respectively. Nest predation and human disturbances were the two main factors affecting breeding success of Emei Shan Liocichlas. Received 13 January 2011. Accepted 22 May 2011.

The genus Liocichla represents a group of Old World babblers found in Asia from India to China, including Red-faced Liocichla (Liocichla phoenicea), Scarlet-faced Liocichla (L. ripponi), Steere’s Liocichla (L. steeri), Emei Shan Liocichla (L. omeiensis), and the newly described Bugun Liocichla (L. bugunorum) (Athreya 2006, Collar and Robson 2007). To date, except for Steere’s Liocichla (Luo 1987; Mays et al. 2006a, b), little has been published on the ecology of the other four species (Collar and Robson 2007). Additional information is needed to provide the basis for their effective conservation (Marzluff and Sallabanks 1998, Ruth et al. 2003).

Endemic to China, the Emei Shan Liocichla is considered globally vulnerable by the IUCN because of a small, declining population and fragmented range (BirdLife International 2010). The species has been recorded only in a few mountainous areas at medium elevations from 1,000 to 2,400 m in south-central Sichuan and extreme northeast Yunnan (MacKinnon et al. 2000, Lei and Lu 2006) on the eastern edge of the Mountains of Southwest China global biodiversity hotspot (Conservation International 2011). Emei Shan Liocichlas often hide in thick bamboo (Chimonobambusa szechuanensis) or deep scrub and are not easy to see in the field (Li 1995). Not surprisingly, its biology and ecology are poorly known. Currently, only a short note of a nest has been reported in the literature (Jiang et al. 2007).

We studied the breeding ecology of Emei Shan Liocichlas in southwest China from March to August 2009 and from April to August 2010. Our objectives were to collect basic information on (1) breeding density, (2) breeding season, (3) characteristics of nesting habitat, nests, eggs, and nestlings, (4) breeding success and influencing factors, and (5) breeding-related behaviors.

METHODS

Study Area.—Most field work was conducted in Laojunshan Nature Reserve, while some supplementary investigations of nesting habitat were in Wawushan Nature Reserve. The two sites are within the distribution area of Emei Shan Liocichla (Li 1995).

Laojunshan Nature Reserve (28° 39' 36"-28° 43' 38" N, 103° 57' 36"-104° 04' 12" E) (Fig. 1) is in the Xiao Liang Mountains between 900 and 2,000 m elevation, covering an area of ~35 km². The climate is temperate with high precipitation (>1,500 mm per year) and relative humidity (>85%), and annual average temperature of 12.4-14.7°C (Liao et al. 2008). The vegetation is characterized by evergreen broadleaf forest, including Castanopsis spp., Schima spp., Camellia spp., Eurya spp., and Rhododendron spp. Some non-native coniferous forests and tea plantations exist at lower elevations (<1,450 m).
Wawushan Nature Reserve (29° 25'–29° 34' N, 102° 49'–103° 00' E) (Fig. 1) is in the Daxianggou Mountains between 1,023 and 3,522 m asl, covering an area of ~365 km². The climate is temperate with average precipitation >2,000 mm per year and relative humidity of 85–90%. The annual average temperature is 10–14°C. The main vegetation type is evergreen broadleaf forest and the dominant trees include Castanopsis platyacantha, Schima sinensis, Lithocarpus viridis, and L. lancea (Bao and Liu 2002). There are also some non-native coniferous forests and tea plantations at lower elevations (<1,650 m).

**Breeding Density.**—The fixed-width transect method (Bibby et al. 2000) was used to estimate breeding density of Emei Shan Liocichlas in Laojunshan Nature Reserve from May to June 2009 and in June 2010. We established 13 transects, each between 1 and 3 km in length, covering a large part of Laojunshan Nature Reserve (Fig. 2). Transects were within primary, secondary, and plantation forests and covered most of the altitudinal ranges within Laojunshan Nature Reserve. Transects were mainly along existing trails and not in inaccessible sites because of steep terrain making it difficult to cover such areas on foot. It was difficult to see the Liocichla in the field due to its secretive nature and the dense vegetation. We detected it mainly by the characteristic songs (a loud and complex whistle) uttered by males. Pilot studies prior to the main survey period showed that male songs of Emei Shan Liocichla could be reliably identified within 200–300 m (varying with terrain and weather). Females did not apparently engage in singing behavior. We only counted males within 150 m along the transects to ensure the accuracy of identification. Those calling from >150 m were also recorded, but not used to calculate densities. Surveys were conducted from 0600 to 0900 hrs in the morning when birds were vocalizing to maintain their territories.

**Nesting Parameters.**—We found nests by observing behaviors and tracking breeding pairs (Martin and Geupel 1993). Nests were numbered when found and recorded with a Global Positioning System (GPS). We visited some nests regularly, following Lu et al. (2008), to examine: breeding season (i.e., the period between the first nest starting construction and the last brood leaving the nest), egg size, clutch size, hatching success (i.e., the proportion of eggs hatched), nestling development, fledging success (i.e., the proportion of young fledged), duration of egg-laying, incubation, and nestling periods, daily nest survival rates (DSR), nest success, and, when possible, causes of nest failure. We recorded altitude, habitat, plant species used, nest-site height, nest concealment, and nest size (if intact) when breeding activity ended for all nests. We also made two daytime (from 0600 to 2000 hrs) observations at one nest during the nestling period using 8 x 35 binoculars at a distance of 13 m to record breeding-related behaviors (e.g., parental...
A white cover board was used to estimate nest concealment following Hoover and Brittingham (1998). We did not measure body size and mass of nestlings to reduce disturbance, but only recorded external morphological characteristics by taking photographs during nestling development. Nests were considered successful if at least one nestling fledged.

Analyses.—We used the nest survival analysis in Program MARK to estimate daily nest survival rates (DSR) (Dinsmore et al. 2002). Nest success was calculated using the Mayfield method (Mayfield 1961, 1975) where the relevant equation is:

\[ \text{nest success} = \text{DSR}^n \]

where \( n \) = the total duration of egg-laying, incubation, and nestling periods. Other analyses were conducted using the statistical package SPSS 13.0 for Windows (SPSS 2004). Data are presented as means ± SE.

RESULTS

Breeding Density and Breeding Season.—Breeding density and breeding season were estimated for Emei Shan Liocichlas in Laojunshan Nature Reserve. The total length of transects was 29 km. We recorded 12 breeding males in 2009 and 16 in 2010 on transects (males were not distributed evenly along the transects). The mean breeding density was 1.20 ± 0.46 males/km\(^2\) in 2009 and 1.55 ± 0.56 males/km\(^2\) in 2010. There was no significant difference between male breeding densities in secondary forest and primary forest (Table 1). We did not find Emei Shan Liocichlas breeding in non-native coniferous forests or tea plantations. The 2009 breeding season was from late April to mid-August (~110 days), while that in 2010 was from mid-May to late August (~100 days). There was no significant difference in duration of the two breeding seasons \( (\chi^2 = 0.476, P = 0.49) \), although the onset of the 2010 breeding season was later than in 2009.

Nesting Habitat and Nest Measurements.—Emei Shan Liocichlas preferred to nest at the edges of or in gaps within natural broadleaf forest, and elevations of nest sites ranged from 1,450 to 1,950 m in Laojunshan Nature Reserve to 1,650 to 2,150 m in Wawushan Nature Reserve. The vegetation around nests included C. szechuanensis, small shrubs, and lianes with few large trees. Twenty-four nests were in bamboo (i.e., C. szechuanensis), four were in small shrubs, three were in roses (Rosa spp.), and three each in bamboo and lianes. Nests were cup-shaped at a mean height above ground of 137.5 ± 4.6 cm \( (n = 34, \text{range} = 60.0–178.0 \text{ cm}) \) and were built mainly by females. Nest measurements varied (Table 2) and materials consisted of fine stems of herbage and liane (and moss for some nests).
TABLE 1. Density of breeding male Emei Shan Liocichlas in Laojunshan Nature Reserve, Sichuan, China in 2009 and 2010 by forest type (primary or secondary). Densities are mean ± SE singing males/km². Densities in primary and secondary forests were compared with a t-test.

<table>
<thead>
<tr>
<th>Year</th>
<th>Secondary forest</th>
<th>Primary forest</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>1.55 ± 0.97</td>
<td>1.55 ± 0.67</td>
<td>0.000</td>
<td>1.00</td>
</tr>
<tr>
<td>2010</td>
<td>2.04 ± 1.07</td>
<td>2.00 ± 0.89</td>
<td>0.033</td>
<td>0.97</td>
</tr>
</tbody>
</table>

bamboo leaves, and aerial roots from the exterior to interior (Fig. 3). Mean concealments above, around, and below nests were 94.4 ± 1.2% (n = 34, range = 70-100%), 92.3 ± 1.1% (n = 34, range = 75-100%), and 62.6 ± 2.5% (n = 34, range = 30-90%), respectively.

**Egg Laying and Incubation.**—There was a short lull of 1-3 days before the first egg was laid after nest-construction was completed. Females laid one egg per day in the morning. Eggs were oval-shaped and eggshell color was glaucous or bright blue, irregularly marked with dark red-brown lines and spots (Fig. 3). Egg measurements varied (Table 2) and mean ± SE clutch size was 2.9 ± 0.2 eggs (n = 10, range = 2-4 eggs). The egg-laying period was ~2-3 days and incubation started after the last egg was laid. Both males and females were observed participating in incubation. The incubation period was ~14 days and hatching success was 58.6% (n = 29).

**Nestling Development and Parental Care.**—Nestling development was relatively fast (Table 3) and both adults provisioned and brooded nestlings. The 28-hr observations for nest 03-2009 at day 3 and day 5 after hatching revealed no significant difference in provisioning rates of nestlings between females and males (female: 3.0 times/hr; male: 4.0 times/hr ) (χ² = 0.143, P = 0.705). However, the number of times and duration of brooding nestlings by the female (n = 38 times; duration = 406 min) were significantly higher than those by the male (n = 18 times; duration = 237 min) (times: χ² = 7.143, P = 0.008; duration: χ² = 44.418, P < 0.001). The nestling period was ~13-14 days. Fledging success was 70.8% (n = 24), and adults continued to provision young after fledging.

**Breeding Success and Influencing Factors.**—Young in eight of 34 nests fledged successfully, 20 nests failed, and the fate of the other six nests was uncertain; the reproductive success was 28.6% (n = 28). The daily nest survival rate (DSR) for nests that contained at least one egg (n = 14) was 0.9565 ± 0.0161 (95% CI: 0.9116–0.9792) and total nest success was 27.5%. Factors influencing nest success were predation (40%, n = 8), abandonment (35%, n = 7), and unknown (25%, n = 5). All nests abandoned were at the nest-building stage, and nest predation occurred in the egg-laying (12.5%, n = 1), incubation (37.5%, n = 3) and nestling (50.0%, n = 4) stages, respectively.

**DISCUSSION**

The Emei Shan Liocichla is highly localized within a small distribution (Li 1995, Dowell et al. 1999, Collar and Robson 2007). It occurred at a low population density of 1.20-1.55 males/km².


<table>
<thead>
<tr>
<th>Measurement</th>
<th>Mean ± SE</th>
<th>n</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest size (cm)</td>
<td>11.33 ± 0.12</td>
<td>28</td>
<td>10.0–12.6</td>
</tr>
<tr>
<td>External diameter</td>
<td>6.95 ± 0.07</td>
<td>28</td>
<td>6.3–7.8</td>
</tr>
<tr>
<td>Internal diameter</td>
<td>5.96 ± 0.12</td>
<td>28</td>
<td>5.0–7.1</td>
</tr>
<tr>
<td>Depth</td>
<td>10.85 ± 0.14</td>
<td>28</td>
<td>9.8–12.5</td>
</tr>
<tr>
<td>Height</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg size and mass</td>
<td>24.92 ± 0.44</td>
<td>11</td>
<td>23.07–28.11</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>17.44 ± 0.11</td>
<td>11</td>
<td>16.98–18.02</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>3.95 ± 0.06</td>
<td>7</td>
<td>3.75–4.21</td>
</tr>
<tr>
<td>Fresh mass (g)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
during 2009–2010 in Laojunshan Nature Reserve. We do not know if the density is typical for this species in other parts of its range.

The clutch size of the Emei Shan Liocichla in our study area was similar to that of Red-faced Liocichla and Scarlet-faced Liocichla (Collar and Robson 2007). However, the clutch size of Steere’s Liocichla is lower (average 2.5 eggs) (Luo 1987). There are other differences between Emei Shan Liocichla and Steere’s Liocichla.

<table>
<thead>
<tr>
<th>Age</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchig</td>
<td>Nestlings largely naked with pink skin and eight clusters of light gray viviparous feathers.</td>
</tr>
<tr>
<td>Day 5</td>
<td>Eyes open and the bottoms of feathers-sheaths light yellow.</td>
</tr>
<tr>
<td>Day 10</td>
<td>Red-yellow wing speculums visible.</td>
</tr>
<tr>
<td>Fledging</td>
<td>Feathers comparatively plump except rectrices with two clusters of light gray viviparous feathers on the head.</td>
</tr>
</tbody>
</table>

including a longer incubation period (16 days) and a shorter nesting period (12 days) in Steere’s Liocichla, and an avoidance of non-native conifer habitat by Emei Shan Liocichlas that does not seem to occur for Steere’s Liocichlas (Luo 1987, Ding et al. 1997). These differences may be related to different adaptive strategies of the two Liocichlas in responding to different environmental factors, such as climate, predators, and intraspecific and interspecific competition.

Nest predation is a common cause of nest failure for birds and can be the main reason for egg and chick loss (Ricklefs 1969, Martin 1993, Thompson 2007). Nest predation was the primary reason for nest failure of Emei Shan Liocichlas — remains of dead chicks or broken egg-shells were found in five nests. Potential nest predators in our study areas include small mammals (e.g., Coloeis c. erythraeus and Mustela sibirica), birds (e.g., Urocissa erythrorhyncha and Garrulus glandarius), and snakes (e.g., Trimeresurus stejnegeri and Elaphe taeniura). Birds have developed many nesting behaviors to reduce the risk of nest predation. For example, some hide their nests or build them in inaccessible sites (Collias and

FIG. 3. Nest and eggs of the Emei Shan Liocichla (Photograph by Yi-Qiang Fu in Laojunshan Nature Reserve, Sichuan, China on 14 June 2009).
Collas 1984). The Emei Shan Liocichla constructed nests in thick bamboo, scrub, or rose bushes with high concealment, which possibly increased the difficulty of their nests being found by predators.

Human disturbance has been suggested as an important factor affecting breeding success (Ruhlen et al. 2003, Arroyo and Razin 2006). Field observations indicated Emei Shan Liocichla readily abandoned nests when they encountered disturbances during the nest-building stage. Disturbance by tourists, rangers, and heekeepers contributed to the abandonment of three nests in our study. The other four nests abandoned were near the path at a mean distance of 1.2 m (range = 0.8-2.0 m), and vegetation around them had clear evidence of disturbance. We believe disturbance by human visitors was the cause of these nest abandonments.

CONSERVATION IMPLICATIONS

Studies have shown that low population density and small geographical range are significantly associated with high extinction risk in declining species (Gaston 1994, Purvis et al. 2000). Thus, the Emei Shan Liocichla would appear to be at risk. The Emei Shan Liocichla is only a provincially protected species in Sichuan despite its IUCN red list status (Vulnerable), and little attention has been given to conservation of this species and its habitat. The Emei Shan Liocichla has been captured and sold in bird markets in Chengdu City, Sichuan Province. We believe the Emei Shan Liocichla should be upgraded to a nationally protected species in China to promote conservation of the species.

Habitat loss and fragmentation are regarded as the major factors contributing to population decline or extinction of many birds (Ribon et al. 2003, Gill 2007). The Emei Shan Liocichla is a forest edge (or gap) species in natural broadleaf forests. However, natural broadleaf forest within its range was commonly replaced in the past by non-native coniferous forests and tea plantations. These habitats were not occupied by Emei Shan Liocichlas, and their spread presents a major threat to the species’ survival. Commercial logging of natural forest has been banned in Sichuan since 1998 (Feng et al. 2008). However, increasing human activities within its range, including tourism development and highway construction, are accelerating fragmentation of the existing habitat of the Emei Shan Liocichla. More attention should be placed on understanding the effect of these changes on the population dynamics of the species. Protecting its existing habitat should be effective for conservation of this species.

Given the sensitivity of the species to human disturbance, we recommend that in nature reserves such as Laojunshan, visitor access to the most suitable nesting areas for Emei Shan Liocichlas should be restricted during the breeding season. Further work is needed to identify the precise habitat requirements of the Emei Shan Liocichla, using a GIS-based approach, both during the breeding season and at other times of the year. A greater understanding of how this species uses its habitats would enhance efforts to conserve them through protection and management of optimal habitat.

ACKNOWLEDGMENTS

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BirdLife International. 2010. Species factsheet: Lioci-
REEBED MANAGEMENT AND BREEDING OF THE MARSH GRASSBIRD IN THE YALU RIVER ESTUARY WETLANDS, CHINA

MING GAO,1,3 XIUQIN YIN,1,4 AND FUXIANG LI2,3

ABSTRACT.—We studied Marsh Grassbirds \textit{(Locustella pryeri sinensis)} and reedbed management from 2006 to 2009 in the Yalu River Estuary Wetlands National Nature Reserve, China. Common reed \textit{(Phragmites australis)} management was monitored and habitat data for 11 variables from 53 nests were collected over a 4-year period. \textit{Calamagrostis epigejos} was replaced by aquatic vegetation, none of the nests existed in 2008, and 10 of 11 habitat variables differed between before deep irrigation (>30 cm depth) (2006 and 2007) and after (2009) due to deep water. Mean ± SD clutch size was 4.5 ± 0.83, the daily survival rate was 92.3%, and overall nest success was 12.5%. Cover of total grasses accounted for 17.7% of the changes in nest height. Reed cutting and irrigation influenced the local breeding population of Marsh Grassbirds. Sound management practices could benefit Marsh Grassbirds and other grassland passerines. Received 29 December 2010. Accepted 6 June 2011.

The Marsh Grassbird \textit{(Locustella pryeri)} breeds on the island of Honshu in Japan (nominate \textit{pryeri}) and in northeast China (race \textit{sinensis}), and possibly in neighboring parts of Russia and Mongolia with records of migrants from the east coast of China and South Korea (BirdLife International 2001). The species is listed as globally vulnerable or near threatened (BirdLife International 2010). It breeds in Eastern Liaoning Province near Chao Yang and in northeast Hebei Province near Qinhuangdao in China, and winters in reedbeds in Hebei Province along the Lower Yangtze River near Hankou (De Schauensee 1984).

Marsh Grassbirds breed in common reed \textit{(Phragmites australis)} marshes and sedge beds in the Far East (Fujita and Nagata 1997). Population sizes are typically small and the species is considered to be declining as a result of wetland destruction in breeding and wintering areas (BirdLife International 2009). Reedbeds have high conservation value in Europe, southern France, and are the major breeding habitat for five passerine species (Poulin et al. 2002). Management of reedbeds is primarily through water control to serve socio-economic rather than conservation interests (Poulin et al. 2002): cut reedbeds have low bird abundance (Poulin and Lefebvre 2002). The null hypothesis in our study was that reed-grass harvest and irrigation do not influence breeding of Marsh Grassbirds. Thus, nests should be well distributed in all reedbeds, and irrigation should not increase reed productivity while decreasing grasses. Nest height should be an important variable to reveal the response of Marsh Grassbirds to irrigation. Our objectives were to describe: (1) changes in Marsh Grassbird abundance, and (2) nest variables to test the alternative hypothesis.

METHODS

Study Area.—The study was conducted in the Dayang River Estuary (39° 52' N, 123° 36' E) of the Yalu River Estuary National Nature Reserve, China (Fig. 1). Dry-grass areas were selected as research sites after being abandoned by reed farmers due to low reed productivity and dense grasses.

We monitored reed production from 2006 to 2009, including timing of irrigation, irrigation water depth, and dry grass and reed cutting.

Data Collection.—Reedbeds were examined for dry-grass patches, and patch boundaries were recorded with a Global Positioning System (GPS) during winter after reed harvest. We searched for nests in all reedbeds during the breeding season along parallel lines at 2-m intervals, and recorded the number of male Marsh Grassbirds observed from late April to mid August. Nest locations were noted with a handheld GPS. The orientation of the entrance of nest-cover was recorded with a compass. Detailed vegetation sampling and habitat measurements were taken after nesting was completed.

Nests were inspected every 3–4 days to check
the number of eggs and/or nestlings. Empty nests were assumed to have been successful (often with 1 egg left after hatching) if the dry skin that flakes off nestlings was present in the nest with minimal disturbance, or if dependent fledglings were present in the vicinity of the nest. Measurements of irrigation water depth (Apr to Jun) and height from nest bottom to ground were recorded, as well as the direction of the entrance to nests. Human scent and disturbances were minimized by using reeds instead of hands to touch nests, and by visiting each nest for < 10 min.

We used the point quadrant (a steel wire of 2-mm diameter with a sharpened tip) to measure percent cover of total grasses following Sutherland (1996). The supporting metal rod was stuck vertically through the vegetation into the soil 10 times per side on four sides of a square (each side being 50 cm in length) around the nest, and readings were taken at the position of each hole in the bar. The presence (touching a grass leaf) or absence readings from the 10-point quadrants were summed to give a score for the entire frame (max = 10). The mean was obtained from readings of four sides based on the assumption that percent cover was unchanged during the breeding period; care was taken to not disturb the vegetation when placing the point quadrant or taking readings.

We used regular sampling methods to measure reed and grass height: the quadrant size was 0.25 m² for grasses and the radius of the sampling circle was 1.5 m for reeds. Five points (4 corners and 1 center) were selected in a square or an inscribed square of the sampling circle, each with four grass plants or two reeds per point. Those
TABLE 1. Differences (Kruskal-Wallis tests) in height and number of reeds in three types of reedbeds, Yalu River Estuary, China. Type 1 = lowland reed marsh, Type 2 = highland reed marsh, and Type 22 = highland reed-grass marsh.

<table>
<thead>
<tr>
<th>Reeds</th>
<th>( \chi^2 )</th>
<th>( p )</th>
<th>Type</th>
<th>( n )</th>
<th>Mean rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>105.183</td>
<td>&lt;0.001</td>
<td>1</td>
<td>40</td>
<td>78.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21</td>
<td>43</td>
<td>109.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>22</td>
<td>53</td>
<td>27.89</td>
</tr>
<tr>
<td>Height</td>
<td>97.197</td>
<td>&lt;0.001</td>
<td>1</td>
<td>47</td>
<td>114.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21</td>
<td>46</td>
<td>80.34</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>22</td>
<td>53</td>
<td>31.48</td>
</tr>
</tbody>
</table>

reeds or grasses nearest to the point were selected if there was no reed or grass at each point. Green and dry reeds (some with inflorescence) height was measured at the point where the reed started to droop above the ground.

Measurement of green grass height was focused on the dominant grass species. The tallest leaf (droop) height for green *Calamagrostis epigejos*, *Juncus gracilis*, and *S. planiculmis* without inflorescence was measured at the portion where the bulk of the mass occurred in the leafy portion of the grass. The inflorescence represents the bulk of the mass for dry *Calamagrostis* and the tallest portion of the inflorescence was measured. However, dry reeds were often broken by wind, and *J. gracilis* and *S. planiculmis* often decayed. Thus, the lowest height values were deleted, and the mean dominant height was used. Counting of reeds occurred in the field, whereas counting of grasses occurred after clipping the nest quadrants. Measurement of the height of green reeds and grasses was in late July.

We used random sampling methods to locate sampling circles (radius = 1.5 m) to count reeds in Type 1 (lowland,  \( n = 55 \) ) and Type 2 (highland,  \( n = 46 \) ) reed marsh. We also measured reed height in the two habitat types with regular sampling methods.

We used GPS to locate dense grass areas and a table of random numbers for defining the sampling point at the intersection of the grids. Cover, height, and number of total grasses between nesting and dense-grass areas were included as there were no nests in dense grass areas.

Statistical Analyses.—Three-independent samples tests were used to compare height and density of reeds among the three types of reedbeds. Two-independent samples tests were used to compare 11 habitat variables between before deep irrigation (30 cm depth) (2006 and 2007) and after (2009), and to compare cover, height, and number of total grasses between nest and dense-grass areas.

Multiple linear regression analysis was used to evaluate which habitat characteristics influenced nest height. Program MARK was used to estimate the daily survival rate and overall nest success. Akaike Information Criterion (AIC) values were calculated in EViews 5 (Quantitative Micro Software 2004) to identify which models best explained the relationship. Nest-entrance orientation data were examined in Oriana 3.21 (Kovach Computing Services 2010), and other data were examined with SPSS 10.0 (SPSS 1999).

RESULTS

Nesting.—Three types of reedbed from the Dayang River to uplands were classified. Type 1, without Marsh Grassbirds, was lowland reed marsh with the tallest reeds and highest reed productivity. Type 2 was highland irrigated reed marsh with shorter reeds and lower productivity separated from the Yellow Sea and the Dayang River by dikes, among which, two subtypes of reed marsh were classified. Type 21 had the densest reed, medium reed height, and productivity. Type 22 had the fewest reeds, the lowest reed height, and productivity (Table 1) as it contained > eight grass species Marsh Grassbirds selected as breeding habitats.

Forty-six of the 53 Marsh Grassbird nests (5 in 2006, 35 in 2007, 13 in 2009) over 4 years had sufficient information for use in nest survival analyses. No nests were found in 2008. Mean (\( \pm SD \)) clutch size was 4.5 (range = 3–6 eggs). The earliest date of laying of the first egg was 22 May and daily survival rate (\( \pm SE \)) was 0.923 (95% CI = 0.055–0.223) across the 26-day nesting cycle.

Twenty-one (39.6%) nests had nest cover with
TABLE 2. Differences (two-independent samples test) between dense grass and nest areas, Yalu River Estuary, China.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Mann-Whitney U</th>
<th>Wilcoxon W</th>
<th>Z</th>
<th>P (1-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cover (n₁ = 20, n₂ = 53)</td>
<td>37</td>
<td>1,468</td>
<td>-6.111</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Height of total grasses (n₁ = 32, n₂ = 53)</td>
<td>17.5</td>
<td>1,448.5</td>
<td>-7.54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Number of total grasses (n₁ = 34, n₂ = 53)</td>
<td>109.5</td>
<td>1,540.5</td>
<td>-6.886</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

An entrance. The mean (= SD) entrance orientation was 296.5 ± 64.1° (n = 21, r = 0.535, P < 0.01), significantly different from the southeast direction of the wet monsoons in this region (χ² = 23, df = 1, P < 0.001). The difference in live or total grasses between nests with and without entrances was significant (U = 157 and 165, W = 388 and 396, Z = -3.256 and -3.11, P = 0.001 and 0.002, respectively).

Nests (n = 41) failed because of predation of eggs and or young. Small mammals were the major cause of nest failure, accounting for 88% (n = 36) of all nest failures. No nests were lost to flooding. The Northern Harrier (Circus cyaneus) was a predominant predator for adult warblers, but not for eggs and nestlings. Common Cuckoo (Cuculus canorus canorus) parasitism did not influence the breeding of Marsh Grassbirds.

Analyses of Variables.—No nests were found in dense Calamagrostis, where cover and number of grasses were significantly different (cover = 97.2 ± 3.0%, density = 574.5 ± 90.6 in 0.25 m², n = 34, P < 0.001) from those at the nest site (Table 2). Nest height was significantly different (U = 116, Z = -2.98, P = 0.003) between irrigation (2006 and 2007) and non-irrigation (2009).

Three models were constructed through multiple linear regression analyses between nest height and other independent variables, and cover, water depth, and dry reed number entered the models successively (Table 3). Model I was best (lowest AICc value) with Y = -6.088 + 0.312X where Y is nest height, X is cover (45% < cover < 100%), and the constant may be considered to be deleted in the equation (r = -0.838, P = 0.406). Ten of 11 variables in 2009 (after deep irrigation) varied (P < 0.05) from those in 2006 and 2007 (Table 4) indicating deeper irrigation decreased grasses and increased reed productivity.

Effects of Reedbed Management.—We searched 18 dry grass patches (5 in 2006, 8 in 2007, and 5 in 2009), which ranged in size from 4 m² to 20,820 m². Mean (= SD) patch size (MPS) was 2,269.5 ± 5,145.2 m², and mean (= SD) number of nests/100 m² was 3.75 ± 6.82. The largest dry grass patch attracted most nests (n = 26 in 2007). Females were often observed searching for nest materials along dikes (7 individuals/200 m) and hillocks, which were dominated by reeds and Phacelurus latifolius when the ground was flooded.

The ratio of live Calamagrostis to total live grass was 77.7% in 2006 and 2007, and the ratio of live J. gracillimus to total live grass was 84.2% in 2009. The ratio of nests constructed with live J. gracillimus to total nests was 7.5% in 2006 and 2007, but 84.6% in 2009 (χ² = 30.017, df = 1, P < 0.001). This suggests the grass community was changed by deeper irrigation (>30 cm). J. gracillimus and S. planiculmis replaced C epigejos in 2009, and deeper irrigation supported fewer males and no nests (Table 5).

DISCUSSION

Our data show that deep irrigation influenced nest placement and success of Marsh Grassbirds as Calamagrostis was replaced by aquatic grasses. Cutting of reeds also influenced nesting of Marsh Grassbirds. The difference in nest height between irrigation (2006 and 2007) and non-irrigation (2009) was significantly different. We infer Marsh

TABLE 3. Ranking of models (dependent variable = nest height; wᵢ is the Akaike weight), to predict Marsh Grassbird use, Yalu River Estuary, China.

<table>
<thead>
<tr>
<th>Model</th>
<th>Constant</th>
<th>r²</th>
<th>F</th>
<th>P</th>
<th>AICc</th>
<th>(Δ)</th>
<th>wᵢ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cover</td>
<td>-6.088</td>
<td>0.177</td>
<td>10.99</td>
<td>0.002</td>
<td>7.288</td>
<td>0</td>
<td>0.357</td>
</tr>
<tr>
<td>Cover + water depth</td>
<td>-5.692</td>
<td>0.275</td>
<td>9.48</td>
<td>&lt;0.001</td>
<td>7.401</td>
<td>0.113</td>
<td>0.342</td>
</tr>
<tr>
<td>Cover + water depth + dry reed number</td>
<td>-5.188</td>
<td>0.346</td>
<td>8.64</td>
<td>&lt;0.001</td>
<td>7.688</td>
<td>0.4</td>
<td>0.296</td>
</tr>
</tbody>
</table>
Grassbirds prefer drier ground over deeper water levels. Predation of nests also influenced nest success as shown by Cain et al. (2006) for other passerines. Claws and other remains were found in failed nests (as also reported by Du et al. 1959), and eggs were regularly lost in five nests; nest conditions remained the same after the eggs were predated. We believe the harvest mouse (Microtus minutus pallipes) was the predator. Harvest mice are classified as a species of 'least concern' in China, and their nests typically are constructed where the vertical structure of the vegetation is significantly denser than average (Bence et al. 2003). The AICc weights ($w_i$) did not converge after the third variable entered the model due to complete separation of data points but cover, water depth, and number of dry reeds influenced nest height. Marsh Grassbirds avoided threats from Northern Harriers by using areas with efficient cover. Flooding may cause Marsh Grassbirds to raise their nests after irrigation. Marsh Grassbirds preferred dry reeds for perches, and live reeds grow in greater quantity in drier reed stands (Spearman’s $r = 0.482, P < 0.01$). Total reed cover at these sites is more dense, taller, and nest height becomes higher.

Live and total grasses at nests with entrances were significantly ($P < 0.01$) less than those with no entrance. Marsh Grassbirds built their nests where cover was considered to conceal their nests better from avian predators.

**CONSERVATION IMPLICATIONS**

Dry-grass patches should be preserved for Marsh Grassbirds (De Schauensee 1984), reeds and grasses should be harvested every 2 years (Valkama et al. 2008), and burning should be prohibited after reed harvest with some rice fields being allowed to revert to reed-grass fields. Marsh Grassbirds adjusted to deeper irrigation water by raising nest height when possible. However, lower nest height (the lowest was 11.69 cm in 2009), may cause nests to be flooded in the rainy season (Jul and Aug). Thus, shallow irrigation with water depth <8 cm (≈ the lowest nest height), should be implemented before 16 May (nest initiation).
which would also benefit migrating wading birds. Additional studies are required to examine detailed reed and grass harvest and irrigation regimes, and control of harvest mouse predation.

ACKNOWLEDGMENTS

Financial support was provided by the Natural Sciences Foundation of Eastern Liaoning University (No. 2006z-18). The authors thank Tianfu Yu, Feng Gao, and K. S. Meldrum of Eastern Liaoning University, and Meifeang Yan, Na Jia, and Zheneno Qu of National Nature Reserve Bureau of Yalu River Estuary Wetlands, Dandong. We especially thank C. C. Elphick, C. E. Braun, and an anonymous reviewer for helpful comments and suggestions for improvement of the manuscript. We thank G. C. White of Colorado State University for helping us to correctly run Program MARK.

LITERATURE CITED


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NESTING RECORD AND POPULATION PHENOLOGY OF THE FLAMMULATED FLYCATCHER (*DELTARHYNCHUS FLAMMULATUS*)

JORGE H. VEGA RIVERA,1 FELIPE CAMPOS-CERDA,1 AND MANFRED MEINERS2

ABSTRACT—We used mist netting in the Chamela-Cuixmala Biosphere Reserve to assess the population phenology of the Flammulated Flycatcher (*Deltarhynchus flammulatus*), a poorly-known dry forest endemic of the Mexican Pacific Slope. We captured 135 birds (first records only) during 23,515 net hrs over a period of several years which suggests this flycatcher is common at the reserve. Monthly averages of captures (including monthly recaptures) differed between seasons with a peak (71%) during May to August (end of dry season to middle of wet season) and fewer (29%) captures during the rest of the year. Flammulated Flycatchers in breeding condition (*n = 38*) were captured in June and July. Hatch year birds (*n = 8*) were captured from 10 July through 11 December. We found an active nest in a cavity on 29 June 2010. We observed pieces of snake skin lining the nest, which may indicate a closer relationship with *Myiarchus*. Additional knowledge on the ecology and breeding biology of the Flammulated Flycatcher is urgently needed for development of effective conservation plans. Received 25 January 2011. Accepted 22 May 2011.

The Flammulated Flycatcher (*Deltarhynchus flammulatus*) is a little known, monotypic species endemic to the Mexican Pacific Region. Its habitat has been described as open thorn woodland dominated by mesquite (*Prosopis* spp.) and acacia (*Acacia* spp.) (Lanyon 1982), semiarid thorn forest, and scrubby woodland (Howell and Webb 1995), or dry woods, scrub, and semi-arid country (Peterson and Chalif 1989). The current known distribution of this species includes the Pacific lowlands of Mexico from Sinaloa south to western Chiapas between sea level and 2,000 m elevation (Miller et al. 1957:82, AOU 1998:407). The Flammulated Flycatcher is generally depicted as an uncommon species within its range. Schaldach (1963:60) reported only two records in his bird surveys for Colima and Jalisco. Bintord (1989:185) described it as a “very uncommon permanent resident in tropical deciduous forest in lower portions of the Pacific Region”. Alvarez del Toro (1980) described it as rare in Chiapas, and Ornelas et al. (1993) observed this species only twice during 2 years of bird surveys in the region of Chamela, Jalisco. This species is listed under the ‘special protection’ category by the Mexican government due to habitat destruction (SEMARNAT 2010). There are also taxonomic reasons for attempting to obtain more extensive information on the species. There has been discussion concerning whether this species should be included in *Myiarchus*, or continue to be treated as a monotypic species of *Deltarhynchus*. The structure of the nest is considered to be critical (Traylor 1977, Lanyon 1982) regarding this controversy. We provide data relevant to the bird’s ecology, life history, conservation, and taxonomic status in western Mexico.

METHODS

Study Area.—This study was conducted at the Chamela Biological Station (3,300 ha), which is part of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico (19° 22’–35’ N, 104° 56’ to 105° 03’ W). The weather is strongly seasonal with well-marked rainy (late Jun to Oct) and dry seasons (Bullock 1986). The Reserve (13,142 ha) is covered predominantly by undisturbed deciduous forest of the Chamela-Cuixmala Biosphere Reserve and of the region in general. The weather is strongly seasonal with well-marked rainy (late Jun to Oct) and dry seasons (Bullock 1986). The Reserve (13,142 ha) is covered predominantly by undisturbed deciduous forest of the Chamela-Cuixmala Biosphere Reserve and of the region in general. There are records of 24 endemic Mexican bird species in the Reserve, 20 of which are restricted to western Mexico (Arizmendi et al. 1990).

Field Procedures.—We conducted mist netting along three trails dominated by deciduous (*n = 2*) and semi-deciduous (*n = 1*) forests characteristic of mature forest of the Chamela-Cuixmala Biosphere Reserve and of the region in general. Mist nets were operated monthly from March 1999 to August 2000 (13,135 net hrs) and at least once a year (mainly but not restricted to the breeding season) in 2001 and from 2005 to 2010 (10,380 net hrs). We placed 8–12 mist nets (12 × 2.5 m, 36 mm mesh size) in a line along each trail, separated from each other by 100 m.
FK3 1. Monthly average captures (standardized by 1,000 net hrs) of Flammulated Flycatchers (Deltarynchus flammulatus) and precipitation at the Chamela Biological Station, 1999-2001, 2005-2010. Error bars represent 1 SD; numbers above bars represent total net hrs sampled by month.

Each captured bird was banded with a numbered aluminum band and processed for body mass (0.1 g with a 50 g electronic scale), exposed culmen and tarsus lengths (0.05 mm using dial calipers), and unflattened wing cord length (0.5 mm using a flat-ended 15-cm ruler). Birds were classified as male or female only if they were in 'breeding condition' (presence of a cloacal protuberance or brood patch). Age was evaluated by the presence of un pneumaticized areas in the skull.

RESULTS

Phenology.—We captured 135 Flammulated Flycatchers (first captures only). Eight were hatching year (HY) and 127 were after hatching year (AHY); 11 were males, 27 were females, and 89 were of unknown gender. Morphological measurements (mean ± SD) of adult Flammulated Flycatchers (n = 29) were: wing chord (71.6 ± 2.25 cm), tarsus (18.1 ± 0.73 cm), culmen (10.2 ± 0.41 cm), and mass (17.2 ± 0.86 g). We did not find gender differences in these metrics (Mann-Whitney U, P > 0.05).

Monthly averages of captures differed between seasons with a peak (71%) during May to August (end of dry season to middle of wet season) and fewer (29%) captures during the rest of the year (Fig. 1). Flammulated Flycatchers in breeding condition (n = 38) were captured only in June and July. HYs (n = 8) were captured from 10 July through 11 December.

Habitat Use.—Comparable numbers of individuals were captured in deciduous forest (n = 59) and semi-deciduous forest (n = 48) based on analysis of data from 1999 and 2000 when we applied equal effort between habitats. There was an interaction among forest type and season ($\chi^2 = 9.2$, df = 1, $P = 0.002$). Proportionately more birds were captured in deciduous forest during the wet season (1:0.55), whereas this relationship reversed during the dry season (0.47:1).

Recaptures.—We recaptured 13 birds; all were captured for the first time during the breeding season and recaptured at the same site during the following breeding season (n = 12) or two breeding seasons apart (n = 1).
Description of Nest and Eggs.—JHVR found an empty Flammulated Flycatcher nest on 29 June 2010 at the Chamela Biological Station (19° 30' 17" N, 105° 02' 26" W, 94 masl). The nest was along the Ardilla Trail on a hillside covered by primary deciduous forest; the canopy height was ~8 m. The nest was inside a cavity of a dead tree (Croton spp., Euphorbiaceae), which was 6 m tall with a DBH of 17 cm (Fig. 2A). The cavity entrance was 2.1 m above ground and measured 8.3 cm wide × 18.2 cm in length. The nest cavity was 7.8 cm wide and 15 cm in length. The nest was lined mostly with thin dark fibers of Spanish moss (Tillandsia usneoides) and rachises (<1 mm in diam) of pinnate leaves (Leguminosae), accompanied by small fragments of dry leaves, shredded bark, an insect wing, small twigs, fungal mycelia, and fragments of snake skin. Man-made materials were absent (Fig. 2B).

The nest had four eggs on 10 and 15 July. There were three nearly fully grown chicks on 27 July and part of the skeleton of the fourth young was still in the nest. The nest was empty and undisturbed on 30 July. Neither eggs nor chicks were visible from the entrance of the nest. We observed a single bird entering or leaving the nest on three occasions. Egg color and shape were similar to those of members of the genus Myiarchus: creamy white with brown circular spots at the wider end of the egg and turning into irregular streaks toward the narrow end. One egg measured 19.41 × 15.84 cm (Fig. 2C).

DISCUSSION

Previous authors (e.g., Schaldach 1963, Binford 1989) described the Flammulated Flycatcher as an uncommon to rare endemic resident along the Mexican Pacific Slope as well as on our specific study area (Hutto 1989, Ornelas et al. 1993). Our data document this species is common during the breeding season and uncommon for the rest of the year, a pattern reported for other species in the Chamela region (Vega Rivera et al. 2003, 2004). This seasonal pattern of occurrence suggests the birds are wary of mist nets, or that at least part of the population undergoes local migrations to habitats not sampled in this study (e.g., secondary forests).

Hutto (1989) during his surveys on 18–28 February 1985 did not find this flycatcher in his study sites outside the Reserve; he reported this flycatcher occurring only in the 'undisturbed' forest of the protected area. Ornelas et al. (1993) suggested the low detection of *D. flammulatus* and other species in Chamela was either because they were rare or because they preferred more humid habitats. Our data suggest this hypothesis may be true as more birds were captured in the semi-deciduous forest during the dry season than in the wet season.

It is evident that long-term studies and simultaneous sampling of a variety of habitats will be necessary to understand the spatial and temporal distribution of birds historically regarded as sedentary.

The end of the dry season seems to mark the beginning of the breeding season for this species and other passerines (Ornelas et al. 1993; Vega Rivera 2003, 2004). We captured 38 birds in breeding condition. However, only 15 females had well-developed brood patches and a partially developed brood patch. These birds were captured between 27 June and 24 July, which corresponds with the beginning of the rainy season and the first annual peak in insect production in Chamela (Lister and Garcia 1992). The only other record for comparison is that of Lanyon (1982) who reported a nesting pair with three eggs on 18 June.

Myiarchus Flycatchers are also cavity nesters, and they incorporate feathers, fur, and shed reptilian skin in the nest lining (Lanyon 1978). Traylor (1977 in Lanyon 1978:414), regarding the relationship of *Myiarchus* and *Deltarhynchus*, wrote: "Unfortunately nothing has been published on the anatomy or behavior of *flammulatus*. If it is found to be a hole nester using a few scraps of snake skin for decoration, it should certainly be merged in *Myiarchus.*" Lanyon (1982) provided the first record of nest and eggs of this species and, to our knowledge, the single published study on this species. Lanyon (1982:421) concluded, "there is nothing in the external morphology, foraging behavior, vocalizations, coloration of the eggs, or the use of a cavity for nesting that would justify generic separation of *Deltarhynchus.*" However, based on the characteristic of the nest, which "being located in a comparatively shallow cavity and in lacking fur, feathers, and shed reptilian skin or substitutes in its conservation", he cautiously concluded that "*Deltarhynchus* should be considered a close relative of the *Myiarchus* assemblage of tyrant flycatchers but merits separate generic status." Our observations regarding the nest of the Flammulated Flycatcher add evidence against this conclusion. The nest's lining included small pieces of skin of an unknown reptilian species and the nest was as deep (15 cm) as those described for *Myiarchus* Flycatchers.
FIG. 2. Nest of a Flammulated Flycatcher (Delichonexus flammulatus) in a tropical deciduous forest, Chanya Biological Station, Jalisco, Mexico. (A) Entrance of the nest cavity (photograph by Manfred Meiners). (B) Nest and egg—the arrow points to a fragment of a snake skin lining the nest. (C) Egg. (D) Young (photograph by Manfred Meiners).
No data exist on population size or trends, but local extirpations and ongoing severe deforestation suggest the species may be declining. Only 27% of the original cover of the tropical deciduous forest remained intact in 1990 in Mexico, and less than 10% of the area covered with deciduous forest is under some type of protection (Trejo and Dirzo 2000; CONANP 2009). Stotz et al. (1996) suggested that severe habitat disturbance in most of the dry forest zones in the Neotropics has greatly affected birds that are deciduous forest specialists. They identified the Flammulated Flycatcher as one of eight conservation 'indicator' species in the tropical deciduous forest of the Pacific lowlands of Mexico, where the Chamela-Cuixmala Biosphere Reserve is the only area protecting this forest type, even though intensive changes in land use are occurring regionally. We hope the information in this paper will aid in conservation efforts for this species and its endangered habitat, encouraging research in annual movements and habitat use of this flycatcher.

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LITERATURE CITED


TAIL PUMPING BY THE BLACK PHOEBE

GREGORY F. AVELLIS

ABSTRACT.—Black Phoebes (Sayornis nigricans) persistently pump their tails vertically while perched but the functional causes are unknown. I address four hypotheses about the function of this behavior in this species: (1) tail pumping aids in balance, (2) tail pumping enhances foraging, (3) tail pumping is a signal to territorial intruders, and (4) tail pumping is a signal to potential predators. The balance (mean ± SE; unstable substrates: 0.23 ± 0.024 pumps/sec, stable substrates: 0.22 ± 0.019 pumps/sec), foraging (non-foraging individuals: 0.28 ± 0.036 pumps/sec, foraging individuals: 0.20 ± 0.026 pumps/sec) and intruder (pre-playback trial: 0.20 ± 0.025 pumps/sec. House Finch [Carpodacus mexicanus] control trial: 0.26 ± 0.029 pumps/sec, Black Phoebe experimental trial: 0.17 ± 0.036 pumps/sec) hypotheses did not significantly explain tail pumping behavior. Tail pumping rates increased during predator sound playback (pre-playback trial: 0.23 ± 0.009 pumps/sec. House Finch trial: 0.26 ± 0.016 pumps/sec, Cooper's Hawk [Accipiter cooperii] trial: 0.61 ± 0.013 pumps/sec, post-playback trial: 0.35 ± 0.013 pumps/sec) and were accompanied by a high amount of both approaches (3.8 ± 0.8) and calls (6.7 ± 1.63). These results indicate that S. nigricans may be using tail pumping behavior as a pursuit-deterrent signal to advertise awareness to potential predators. Received 18 January 2011. Accepted 26 May 2011.

A signal is any trait used for communication among individuals that modifies the behavior of a receiver and is useful to both the signaler and the receiver (Krebs and Davies 1993). Signals in many species can aid as a predator deterrent, territory defense, and/or in the context of sexual selection among other reasons. Avian tail movements may function in one of these contexts. Wood (1974) found a higher tail flicking rate in Common Moorhens (Gallinula chloropus) when a predator was nearby and Alvarez (1993) and Alvarez et al. (2006) noticed faster flicking rates in healthier individuals. Moorhen tail movements may operate in a sexual context as the study was performed before the breeding season, but Alvarez et al. (2006) suggested they function to provide information about physical condition to predators and require less energy than evading a predator. Murphy (2010) suggested tail wagging in Turquoise-browed Motmots (Eumomota superciliosa) may function in territory maintenance.

Tail movements may not function as a signal but instead serve to enhance foraging or balance. Willie Wagtails (Rhipidura leucophrys) used tail movements when foraging because they startled and displaced insect prey (Jackson and Elgar 1993), and Smith (1969) hypothesized that tail movements by Eastern Phoebes (Sayornis phoebe) could help maintain balance.

Black Phoebes (S. nigricans) persistently pump their tails by quickly lowering and raising them (Fitzpatrick et al. 2004) and the function of this behavior is poorly understood. The objective of my study was to demonstrate the potential causes of this behavior by testing the following hypotheses previously addressed by Carder and Ritchison (2009) for Eastern Phoebes: tail pumping aids in balance, enhances foraging, signals territorial behavior, and is a signal to predators. A hypothesis of a sexual context was not considered because both male and female Black Phoebes tail pump throughout the year (pers. obs.).

The following predictions were made: higher pumping rates would be observed on 'unstable' substrates, higher rates should be correlated with more foraging attempts and/or successful outcomes, Black Phoebes should tail pump at higher rates when a potential competitor is present, and faster pumping rates would be observed in the presence of a potential predator.

METHODS

Study Species.—The Black Phoebe is a small (16–18 g) insectivorous passerine bird that forages primarily in aerial sallies and often returns to the perch of origin (Fitzpatrick et al. 2004). Territorial males can often be heard singing, and are resident on the study area.

Study Area.—All data were collected at sites in Wildwood Regional Park in the Arroyo-Conjio Valley, California, USA (34.2° N, 118.9 W). 'Lizard Rock' is an open grassland-type habitat consisting of mainly tall grasses, sparse bushes, and no tree canopy. 'Oak Grove' is a semi-open woodland habitat consisting of a moderate amount
of tree canopy, 'Paradise Falls' is a riparian habitat consisting of dense foliage and a high percent of tree cover. Observations were made on 3 days between 0700 and 1500 hrs PST during February and April 2010. All observations were performed on individuals at one study site, each site was the focus of 1 day, and each site was observed only once. Three individuals were observed within both ‘Lizard Rock’ and ‘Paradise Falls’ and four individuals were observed at ‘Oak Grove’. Observations were the method used because birds were not banded or otherwise individually marked; sample size was kept small to avoid pseudoreplication.

Tail pumping rates were calculated by dividing the number of tail movements by the duration of the observation period. A tail movement consisted of a downward flick followed by an upward flick. Recordings were made of six House Finches (Carpodacus mexicanus) and six Black Phoebes within the study location with an Olympus LS-10 PCM recorder and Olympus ME-30 omni-directional microphone in the .mp3 format at 320 kb/sec and 44.1 kHz. Playback experiments consisted of recordings from individuals separated at least 300 m from a focal individual to eliminate bias that may result from neighbor familiarity. A prerecorded Cooper’s Hawk (Accipiter cooperii) vocalization (Keller 2003) was used for anti-predator response experiments because no potential predator vocalized in the field. This may represent a source of pseudoreplication, but responses to this stimulus were observed from several different birds from three different sites. All recordings were edited with Raven Lite (Charif et al. 2006) to ensure a uniform (3 min) playback time and to eliminate background noise and silence. Playback experiments were performed using an iPod and iHome speakers hidden from sight and controlled with a remote. Playlists of House Finches and Black Phoebes were played with the random order function of the iPod selected. Focal individuals were males that had been observed singing (i.e., territorial).

Balance Hypothesis.—Tail pumping rates were compiled from trial data that included observation periods used for the foraging enhancement hypothesis plus observations made during pre-playback trials for the two experimental tests. Seventy observations among 10 individuals (mean ± SE, 7.1 ± 0.89 observations/individual) were compared between types of substrate. A ‘stable’ substrate consisted of those judged to support the weight of an individual Black Phoebe (e.g., ground, rocks, fences, etc.). Three 5-g fishing line weights were tied to the substrate when stability could not be judged and, if any displacement resulted, the substrate was categorized as ‘unstable’. This method was used to mimic displacement of perches by the mass of an individual bird. If a questionable substrate was out of the reach of the observer, it was eliminated from analysis.

Foraging Enhancement Hypothesis.—Tail pumping rates were calculated by counting tail movements of 10 individuals in 50 observations (mean ± SE, 5.0 ± 0.86 observations/individual) for up to 10 min each. The trial was discontinued if an individual left the view of the observer. Whether or not an individual foraged during this trial was noted and foraging outcome of those that did forage was also recorded.

Signal to Territorial Intruders Hypothesis.—Tail pumping rates were calculated by observing tail movements of 10 individuals in each of four trials consisting of 3 min each and separated by 30 sec. The ‘pre-playback’ trial consisted of no manipulation, the ‘control’ trial consisted of recorded House Finch vocalizations being played to a focal individual Black Phoebe, the ‘intruder’ trial consisted of a recorded Black Phoebe being played to a focal individual, and the ‘post-playback’ trial consisted of the ‘intruder’ vocalization being turned off. Whether or not a focal individual called or approached the sound source for each trial was also noted. An approach was defined as an individual moving within 2 m of the speakers and approach proportions were calculated by dividing the number of approaches by the number of observations for each trial.

Signal to Predators Hypothesis.—Tail pumping rates were calculated by observing tail movements of 10 individuals in each of four trials consisting of 3 min each and separated by 1 min. The ‘pre-playback’ trial consisted of no manipulation, the ‘control’ consisted of recorded House Finch vocalizations being played to a focal individual phoebe, the ‘predator’ trial consisted of a recorded Cooper’s Hawk being played to a focal individual, and the ‘post-playback’ trial consisted of the predator sound being turned off. Whether or not a focal individual called and/or approached the sound source was noted for each trial, and proportions were calculated by dividing the number of approaches and calls by the number of observations for each trial. An approach was
defined as an individual moving within a 2-m radius of the speakers.

Site Impact.—Data from the pre-playback and control (e.g., House Finch vocalization) trials were analyzed with repeated measures ANOVA. Individuals, sites, and individuals within sites were included in the model as random factors.

Statistical Analyses.—All hypotheses consisted of observations of 10 individual birds. Data were analyzed by a GLM with substrate type as the fixed factor and individual as the random effect for the balance hypothesis. A t-test was used to examine whether foraging birds used higher tail-pumping rates than non-foraging individuals, and logistic regression was used to test whether successful foraging could be predicted by tail-pumping rate. Tail pumping rates were analyzed with a GLM for the intruder hypothesis with vocalization type as the fixed factor and individual as the random factor. Interactions between the fixed and random factor, if not statistically significant ($P > 0.25$), were dropped from the analysis and the main effect of vocalization type was analyzed by ANOVA with a Tukey post-hoc test. A $G^2$ test was used for approach and call proportions, and Pearson's $r$ was used to examine correlations between the number of approaches and calls. Data were transformed as appropriate to meet statistical assumptions and analyses were performed with Systat 11 (Systat 2004). Tail pumping rates are reported as means ± SE.

RESULTS

Balance Hypothesis.—There were no significant differences in tail pumping rates, controlling for the effects of individuals, between birds perched on 'stable' substrates and those perched on 'unstable' substrates ($F_{1,60} = 0.023, P = 0.88$).

Foraging Enhancement Hypothesis.—Tail-pumping rates were similar between foraging and non-foraging individuals ($t_{45} = -0.85, P = 0.40$). However, the probability of success of those eight individuals that did forage could be predicted by tail pumping rate (logistic regression deviance $G^2 = 4.44, df = 1, P = 0.035$; Fig. 1). Increased foraging success was shown by those individuals that tail pumped at a lower rate.
FIG. 2. (A) The highest proportion of Black Phoebes approaching the sound source was in the 'intruder' trial, and (B) tail pumping rate was significantly lower when a recorded Black Phoebe was used in the playback trial. Different letters above error bars denote a significant difference by the Tukey post-hoc test.

Signal to Territorial Intruders Hypothesis.—No individuals produced a call when this hypothesis was tested. There was a difference in whether an individual approached the hidden speaker among all playback trials ($\chi^2 = 24.27, df = 3, P < 0.001$; Fig. 2A) and, after the interaction between playback type and individual was dropped from the analysis ($F_{3,39} = 18.72, P < 0.001$; Fig. 2B). The highest proportion of approaches and lowest tail pumping rates were observed when a conspecific vocalization was played.

Site Impact.—Tail pumping rates were significantly different among sites (Fig. 3), whereas individuals and individuals within sites were not different. Black Phoebes at ‘Lizard Rock’ had the greatest tail pumping rates.

Signal to Predators Hypothesis.—There were differences in the amount of calls ($\chi^2 = 20.61, df = 3, P < 0.001$) and approaches ($\chi^2 = 20.12, df = 3, P < 0.001$) among playback types (Fig. 4), a positive correlation between the number of calls and approaches ($r = 0.63, P < 0.001$), and a difference in tail pumping rates among playback types ($F_{3,39} = 175.1, P < 0.001$; Fig. 4) after the interaction of playback type and individual was dropped from the analysis ($F_{3,27} = 0.93, P = 0.43$). Approaches, calls, and tail pumping rates were greatest when the Cooper's Hawk vocalization was played.

DISCUSSION
Balance Hypothesis.—Black Phoebes did not pump their tails to maintain balance, which has been demonstrated in a variety of avian species. Bearded Reedlings (Panurus biarmicus) with experimentally manipulated tail lengths did not differ in their ability to balance on unstable substrates when compared to controls (Romero-Pujante et al. 2005). Carder and Ritchison (2009) found similar tail pumping rates for Eastern Phoebes on different substrate types (stable vs. non-stable) and no correlation between tail movements and wind velocity. Tail pumping occurs in only a small percent of perching birds (Carder and Ritchison 2009) and is probably not used to maintain balance.

Foraging Enhancement Hypothesis.—Tail pumping did not predict foraging behavior of Black Phoebes. However, of those birds that did forage, successful bouts declined as tail pumping increased. Similarly, Eastern Phoebes (Carder and Ritchison 2009) and White Wagtails (Motacilla alba) (Randler 2006) did not move their tails more often when foraging. Randler (2006) found a negative relationship between tail movement and foraging rates, and a positive relationship between tail movements and...
FIG. 4. The highest proportion of (A) calls and (B) approaches by Black Phoebes was observed when the Cooper’s Hawk vocalization was played. (C) The highest tail pump rate was observed when the Cooper’s Hawk call was played. Different letters above error bars denote a significant difference by a Tukey post-hoc test.

vigilance behavior. The results of my study suggest Black Phoebes are less successful at foraging when they are more vigilant.

Signal to Territorial Intruders Hypothesis.—Black Phoebes pumped their tails at a significantly lower rate when an apparent intruder was detected, and may maintain their territory by chasing the intruder. Tail flicking by Moorhens was found to decrease after an individual was played a recording of a conspecific (Randier 2007), and Weeks (1994) observed that Eastern Phoebes territorial maintenance behaviors consisted of chasing the intruder while calling.

Signal to Predators Hypothesis.—There were differences among the three sites. The greatest tail pumping rate was at ‘Lizard Rock’, an intermediate rate at ‘Oak Grove’, and the lowest rate at ‘Paradise Falls’. Raptors were observed soaring above ‘Lizard Rock’ on several occasions but not above the other two sites. Thus, individuals in the exposed habitat of ‘Lizard Rock’ may be under a greater amount of predation pressure and use tail pumping as a means to advertise awareness of predators.

Black Phoebes tail pumped at significantly higher rates when a predator call was played, and approached the speaker and called more often during the predator’s call; these approaches and calls were positively correlated. Thus, Black Phoebes use tail movements as a signal to predators, probably as a correlate of intention of impending flight. Similarly, tail movements have been demonstrated as anti-predatory behavior in Common Moorhens, which tail-flicked more often not only when a predator was seen but also when it was heard (Randier 2007). Carder and Ritchison (2009) demonstrated that Eastern Phoebes tail pumped, called, and approached a visible predator at higher rates. My study demonstrates that sound, in addition to vision, is an important component in Sayornis signaling behavior as responses were observed at highest rates when a potential predator vocalized. Multiple cues used by prey to signal awareness of a predator have been
demonstrated for many species (Alvarez et al. 2006, Murphy 2006, Randler 2007) in addition to Black Phoebes.

The array of behaviors studied probably advertises the overall condition of an individual in addition to signaling awareness of a predator. Zahavi’s (1975) handicap principle postulated that signals are honest because of the inherent cost of these behaviors. Individuals, therefore, do not cheat because signal quality is related to body condition (Zahavi 1977, Hasson 1991, Hasson 1994). Black Phoebes that tail pump, call, and approach are likely advertising they are healthy individuals and are difficult to capture. Black Phoebes are highly maneuverable birds and these energetically costly behaviors most likely reflect their low profitability as prey.

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LITERATURE CITED

INFLUENCE OF HATCH ORDER ON BEGGING AND PLUMAGE COLORATION OF NESTLING EASTERN BLUEBIRDS

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ABSTRACT.—Hatching asynchrony in altricial songbirds can influence the morphology and behavior of nestling birds. We compared the position of nestling Eastern Bluebirds (Sialia sialis) in the hatching hierarchy to their (1) position in the egg-laying order, (2) rate of nestling begging, (3) circulating corticosterone, (4) size, and (5) plumage coloration. Most nestlings hatched within 36 hrs of each other, and nestlings hatched in the order in which eggs were laid. Early-hatched nestlings were heavier than late-hatched nestlings for the duration of the growth period and begged less intensely than their late-hatched siblings. There was little evidence of severe effects of hatch order. Hatch order did not influence nestling corticosterone levels nor did we find effects of hatch order on ornamental plumage coloration. Our data suggest no long-term effect of hatching asynchrony on the development of sexually selected plumage coloration.

Hatching asynchrony is common in many species of birds and results from incubation prior to clutch completion. Early-hatched nestlings are generally older and larger than their later-hatched siblings which creates a size hierarchy within the nest with early-hatched nestlings assuming a dominant role as later-hatched nestlings often grow slower (Clotfelter et al. 2000, Nilsson and Gardmark 2001, Saino et al. 2001, Magrath et al. 2003). Size hierarchies within broods often create differences in need for food among siblings, and offspring can use behavioral strategies to alter the rate at which they are provisioned. Nestling begging has been found to be an honest indicator of need (Price and Ydenburg 1995, Lotem 1998, Saino et al. 2000). Successful begging behavior usually results in acquisition of more food and translates into an increase in mass (Kilner 1995).

Hormones may be the proximate mechanism underlying variation in begging behavior. The nutritional state of nestlings is negatively correlated with activity of the hypothalamus–pituitary–adrenal axis in several species of seabirds (Nunez-de la Mora et al. 1996; Kitaysky et al. 1999, 2001a). Experimental elevation of corticosterone has been shown to cause increased begging rates of nestling Black-legged Kittiwakes (Rissa tridactyla) (Kitaysky et al. 2001b). Late-hatched nestlings are assumed to experience nutritional stress and are expected to increase corticosterone secretion, which in turn, should increase begging behavior (Marra and Holberton 1998, Kitaysky et al. 1999).

Nestling condition also can be honestly signaled by plumage coloration (Fitze et al. 2003, Tschirren et al. 2003, Jucot and Kempenaers 2007, Siefferman and Hill 2007). Juvenile plumage coloration might function in parent-offspring communication and mediate parental favoritism either at the nest (Tschirren et al. 2003, Galvan et al. 2008, Grigio et al. 2009) or later during the post-fledgling dependence period (Tanner and Richner 2008, Ligon and Hill 2010). Nestling condition can have long-term effects by influencing adult plumage used in sexual signaling, if nestlings retain portions of the juvenile plumage into adulthood. Parental strategies for maximizing fitness may include adjusting the relative investment in juvenile males and females (Trivers and Willard 1973) by manipulating their positions in the laying order (Badyaev et al. 2002).

Eastern Bluebirds (Sialia sialis) are sexually dichromatic songbirds that, on average, lay 4-5 egg clutches in Alabama. Males display bright UV-blue structural coloration on the plumage of their back, head, wings and tail while females display similar coloration but are duller overall. Brighter individuals gain higher reproductive success as adults (Siefferman and Hill 2003, 2005). Bluebirds in Alabama begin incubation on...
the day the female lays the penultimate egg (M. Liu, unpubl. data). Incubation lasts —15 days, and all nestlings in the brood hatch over a period of between 6 and 36 hrs (Gowaty and Plissner 1998).

The rectrices and remiges of nestling bluebirds begin to emerge within 11 days after hatching and exhibit UV-blue ornamental coloration. The color of remiges can be quantified by 14 days after hatching (Siefferman and Hill 2007). Young bluebirds retain these juvenile wing and tail feathers as part of their first nuptial plumage (Gowaty and Plissner 1998). Experimental manipulations of food availability to nestlings demonstrate that male nestling bluebirds reared in poor natal conditions grow more slowly and display duller wing color compared to those reared in better natal environments (Siefferman and Hill 2007). Parents exhibit preferences for the more colorful fledglings (Ligon and Hill 2010).

Our objectives were to: (1) test the assumption that laying order reflects hatching order, (2) investigate whether sex ratio varies between early- and late-hatched nestlings, (3) ascertain whether late-hatched chicks remain smaller than early-hatched siblings throughout the hatching period, (4) test whether late-hatched nestlings have higher circulating corticosterone and beg more vigorously than their early-hatched siblings, and (5) investigate whether late-hatched nestlings have duller plumage coloration than their early-hatched siblings.

METHODS

Study Area and Field Procedures.—We studied a population of Eastern Bluebirds breeding in nest boxes in Lee County, Alabama, USA (32°35'52" N, 85°28'51" W; elevation 216 m) in 2007. The study site includes pasture and edge habitat. We monitored first nests of Eastern Bluebirds every other day during the nest building stage. We visited nests each day during the laying period and marked each new egg with a Sharpie® marker to establish laying order. We identified two groups of eggs in each brood in relation to laying order, defined as early- and late-laid eggs. Eggs laid in the first half of the clutch were early-laid in clutches with even number of eggs and those laid in the last half were late-laid eggs. The middle egg was considered a late-laid egg in nests with an odd number of eggs.

We ascertained which chick hatched from each egg during the hatching period by visiting each nest every 3 hrs (0600—1900 hrs) during daylight until all eggs hatched. We identified individual nestlings by marking their tarsi with a unique color of Sharpie® marker. Nestlings were assigned the same hatching order if more than one egg hatched in the same 3-hr interval but were given different markings.

Nestlings that hatched in the first 3-hr interval during which hatching occurred were 'early-hatched nestlings'. These were nestlings with early spots in the hierarchy of hatching positions. Similarly, nestlings that hatched after the first 3-hr hatching interval were 'late-hatched nestlings'. These were nestlings with late spots in the hierarchy of hatching positions. We monitored >200 clutches but were only able to assign egg laying and nestling hatch order to 31 broods because most eggs hatched during the night.

We defined the age of the brood by the hatching date of the first-hatched nestling (day 1 = hatch day). We measured mass of nestlings to the nearest 0.1 g on day 2, 5, 8, 11, and 14 post hatch. We banded nestlings at 8 days of age and collected a 150-ul blood sample within 3 min of first handling each nestling. We spun the blood sample in a centrifuge, separated the sera and plasma, and froze the samples. We measured the right tarsi and wing to the nearest 0.1 mm at day 14 post hatch. Nestlings increase rapidly in mass from hatching until they are about 11 days of age, but by 13 days of age, the mass of nestlings begins to reach the asymptote (Pinkowski 1975). Thus, mass at 14 days is an accurate estimate of fledging mass. Nestlings generally fledge between 15 and 18 days post hatch.

Nestlings at 8 days of age have feather sheaths. Feathers begin to emerge from the feather sheaths at 11 days of age and 2 cm of the feathers have emerged from the sheaths at 14 days of age. We cut the distal 2 cm of both primary 5 feathers of nestlings for spectrophotometric plumage analysis on day 14 post hatch. We stored the feathers in envelopes in a climate-controlled environment until spectrophotometric analyses were conducted. Juvenile Eastern Bluebirds are sexually dichromatic. We classified male and female nestlings using sexually dichromatic plumage coloration. Previous experience with plumage coloration and molecular classification showed that 95% of young could be properly classified using plumage coloration (L. Siefferman, pers. obs.).

Nestling Begging Behavior.—We stimulated nestlings to beg and video recorded nestling begging behavior in the morning when the oldest
nestlings were 5 days of age. Nest holes were first blocked for 30 min prior to recording behavior to ensure that no nestlings were satiated. Nestlings were removed from the nest box and placed in a cup with nesting material. A researcher stimulated the nestlings every 30 sec for 5 sec over the duration of 3.5 min by gently rattling the cup and whistling.

One researcher (NS) quantified begging behavior of individual nestlings through measurements of begging intensity. We scored the maximum posture to measure intensity during each trial as 0 = not begging; 1 = mouth open; 2 = mouth open, head back; 3 = mouth open, head back, neck stretched; 4 = mouth open, head back, neck stretched, back vertical. We summed the intensity rankings for each nestling to assess the overall begging intensity during the trial; thus, begging intensity includes both frequency and degree of begging.

Reflectance Spectrometry.—One researcher (LS) recorded spectral data with an Ocean Optics S2000 spectrometer (range = 250–880 nm; Dunedin, FL, USA) and a light source illuminated with both a deuterium bulb (UV light source) and a tungsten-halogen bulb (visible light source). We generated reflectance data relative to a WS-2 white standard (Labsphere Inc., North Sutton, NH, USA) and placed a micron fiber-optic probe at a 90-degree angle 1 mm from the feather surface. Reflectance data were summarized by calculating two standard descriptors: brightness and UV-chroma. Brightness was calculated as the mean of the summed reflectance from 300 to 700 nm and UV-chroma as the proportion of the total reflectance that is in the ultraviolet range (300–400/300–700).

Hormone Analyses.—Serum corticosterone and testosterone were extracted and separated using celite column chromatography following methods modified from Schwabl (1993). Briefly, 20 µl of serum was mixed with 3 ml diethyl ether, vortexed, and allowed to settle for 20 min. Samples were snap frozen and the liquid portion containing the steroid hormones was reserved and dried using a N₂ stream. Samples were re-suspended in 1 ml of 10% ethyl acetate in isooctane (VanWatersRogers, Suwanee, GA, USA) after which steroid hormones were eluted through the columns in the following fractions of ethyl acetate in isooctane: dihydrotestosterone -10%, testosterone -20%, and corticosterone -30%. Samples were further dried using a N₂ stream, and testosterone and corticosterone were quantified using a competitive binding radioimmunoassay following Wingfield and Farner (1975). Testosterone recoveries averaged 60%; however, testosterone was below detectable levels in all samples, and testosterone concentrations were not used in analyses. Corticosterone recoveries averaged 70%, and intra-assay variation was 4.9.

Statistical Analyses.—We tested whether laying order predicted hatching order and whether the sex ratio within broods differed between early- and late-hatched nestlings using Generalized Linear Models with binomial error distribution and logit link. We performed Linear Mixed Effect Models to analyze the effects of early- versus late-hatching on begging behavior, corticosterone level, structural size, and plumage coloration. All models include gender of the nestlings and early-versus late-hatching as fixed factors, brood size as a covariate, and nest as the random factor. We performed a mixed-effect model to analyze the effects of the early-versus late-hatching on juvenile body mass (measured at ages 2, 5, 8, 11, and 14 days). The model included gender of nestlings and early- versus late-hatching as fixed factors, age and brood size as covariates, and nest as the random factor. We used a stepwise backward procedure for simplification of the mixed models and tested two-way interactions between the covariate and the fixed factors. Data were normally distributed. None of the interaction terms was significant (P > 0.05) and interactions were removed from models. SPSS (2006: Version 15.0) software was used to analyze data and all tests were two-tailed.

RESULTS

Brood Size and Incidence of Brood Reduction.—Seven of 31 clutches had a total of two nestlings each, nine had three nestlings, nine had four nestlings, and six had five nestlings. Seventeen percent of the 208 Eastern Bluebird nests we monitored experienced total nest failure. Eight percent of the 172 successful nests (at least 1 nestling fledged) had one or more nestlings die from apparent starvation. We were able to identify whether the dead was an early- or late-hatched nestling in nine nests; 44% were early-hatched nestlings and 56% were late-hatched nestlings.

Laying Order, Hatching Order, Hatching Span, and Nestling Gender.—Laying order predicted hatching order (Wald X² = 14.46, n = 31, P < 0.001); 90% of late-laid eggs resulted in lat-
TABLE 1. Effects (estimates ± SE) of hatch order and gender on concentration, and plumage coloration traits of nestling Eastern Bluebirds.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Factor</th>
<th>Estimate ± SE</th>
<th>df</th>
<th>F</th>
<th>p</th>
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</thead>
<tbody>
<tr>
<td>Mass (g)</td>
<td>Hatch order</td>
<td>1.24 ± 0.24</td>
<td>1, 525</td>
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<td>1, 525</td>
<td>5.734</td>
<td>&lt;0.001</td>
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<td>Brood size</td>
<td>-0.34 ± 0.11</td>
<td>1, 525</td>
<td>9.37</td>
<td>0.002</td>
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<tr>
<td>Tarsus length (mm)</td>
<td>Hatch order</td>
<td>0.46 ± 0.52</td>
<td>1, 85.0</td>
<td>0.77</td>
<td>0.38</td>
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<td>1, 85.0</td>
<td>0.72</td>
<td>0.40</td>
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<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Brood size</td>
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<td>1, 85.0</td>
<td>1.27</td>
<td>0.26</td>
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<td>Wing length (mm)</td>
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<td>1.01 ± 0.42</td>
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<td>5.79</td>
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<td>0.20 ± 0.56</td>
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<td>0.72</td>
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<td>Begging intensity</td>
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<td>Gender</td>
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<td>Brightness (%)</td>
<td>Hatch order</td>
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<td>&lt;0.001</td>
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<td>UV chroma (%)</td>
<td>Hatch order</td>
<td>0.05 ± 0.01</td>
<td>1, 66.9</td>
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<tr>
<td></td>
<td>Gender</td>
<td>-0.01 ± 0.01</td>
<td>1, 66.9</td>
<td>110</td>
<td>0.003</td>
</tr>
</tbody>
</table>

* Estimates are relative to late-hatched nestlings.
† Estimates are relative to males.

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Effect of Hatch Order and Gender on Nestling Size, Begging Behavior, and Hormones. —Early-hatched nestlings were significantly (P < 0.001) heavier than late-hatched nestlings throughout the nestling period (no significant age × hatch order interaction; P = 0.83), brood size negatively affected mass, and we found no effect of gender on mass (Table 1; Fig. 1). Late-hatched nestlings begged significantly more vigorously than their early-hatched siblings, but neither brood size nor gender influenced begging rates (Table 1; Fig. 2). We found no effect of hatch order, gender, or brood size on nestling corticosterone levels (Table 1). We also found no difference in length of tarsi of early- and late-hatched nestlings at 14 days of age, but early-hatched nestlings had longer wings (Table 1). Hatch order did not significantly influence either brightness or chroma of plumage coloration. However, males were significantly more colorful than females and nestlings from smaller broods were more colorful than those from larger broods (Table 1).

DISCUSSION

We were able to identify the hatching order of all eggs in only ~15% of the clutches despite close monitoring for hatching, demonstrating that many nestlings hatch during the night and many clutches hatch synchronously in this population of Eastern Bluebirds. Thus our data may represent nests with the greatest hatching asynchrony. Position in laying order was a strong predictor of position in hatching order, and hatching order influenced the morphology and behavior of nestlings. Late-hatched siblings had lower mass compared to their early-hatched siblings throughout the nestling period, and late-hatched nestlings begged more vigorously than early-hatched nestlings at 5 days of age. Late-hatched nestlings were lighter in mass and had shorter wing length near the age of fledging. It is possible that late-hatched nestling bluebirds are more likely to experience post-fledging mortality compared to their older
siblings as larger body mass and wing length influence post-fledging survival in other species of altricial birds (Råberg et al. 2005). We failed to detect any interaction between hatch order and gender, and found no effect of hatch order on nestling corticosterone or plumage coloration. Lack of effect of hatch position on stress hormones and color suggest that late-hatched chicks may not have experienced extreme stress as a result of hatching position.

Studies of other species of birds also found laying order can be a strong predictor of hatching order (Beissinger and Wallman 1991, Clotfelter et al. 2000, Saino et al. 2001). This relationship is expected when females commence incubation prior to laying of the final egg (Magrath 1990). Laying order affects hatching order, and female bluebirds could potentially strategize their investment in eggs from different positions in the laying sequence to compensate for chick disparity caused by hatching asynchrony. Thus, although females could have differentially invested in eggs from different positions in the laying sequence to compensate for chick disparity caused by hatching asynchrony, we found no evidence of a greater incidence of males hatching early. Our observations are similar to those of Lombardo (1982) for Eastern Bluebirds and Koenig and Dickinson (1996) for Western Bluebirds (Sialia mexicana), who also found no evidence of sex ratio bias associated with environmental conditions.

Early-hatched nestlings were significantly larger than their late-hatched siblings throughout the growth measurement period (up to day 14). The early fledgling period is a time of high mortality in passerine birds (Sullivan 1989), and all siblings in a brood tend to fledge on the same day (L. Siefferman, pers. obs.); thus, nestlings with relatively shorter wings may be less able to survive the fledgling period. We found no evidence that bluebirds in our population use a strategy of brood reduction; nestlings that appeared to die of starvation were no more likely to have hatched early or late in the clutch. Bluebirds in our study population experienced low incidence of nestling starvation compared to birds in other studies (Kendeigh 1942, Pinkowski 1977).

Hatching asynchrony created differences in begging rates among Eastern Bluebird nestlings: the late-hatched nestlings likely experienced greater need for food as they had lower mass and begged more than their early-hatched siblings. Begging has been shown to be an honest signal of need in other passerine species (Mondloch 1995, Price and Ydenburg 1995, Lotem 1998, Saino et al. 2000). Late-hatched nestlings did not have higher concentrations of circulating corticosterone at 8 days of age. Past experiments demonstrate that corticosterone promotes nestling begging (Kitaysky et al. 2001b, Loiseau et al. 2008). Corticosterone concentrations in those studies mimicked levels exhibited by nestlings during
extreme food shortages (Kitaysky et al. 2001a). Thus, late-hatched Eastern Bluebirds were not likely experiencing extreme food shortage as glucocorticoid concentrations do not suggest a high level of stress. Hatching later in the brood may not be extremely stressful for Eastern Bluebirds. Our data should be interpreted with caution because corticosterone levels and associated responses by nestlings can vary across development (Schwabl 1999, Sockman and Schwabl 2001), and we did not measure circulating corticosterone and begging on the same day.

Early-hatched chicks were larger than late-hatched nestlings, but hatch order did not influence plumage coloration. Past research suggests UV-blue structural coloration is a condition-dependent trait in nestling Eastern Bluebirds that can be negatively influenced by natal stress induced by environmental increases in brood size (Siefferman and Hill 2007). We found nestlings reared in larger broods weighed less and were duller compared to those reared in smaller broods, suggesting some effect of natal environment on nestling coloration. It may be that conditions created by hatching asynchrony are not sufficiently costly to negatively affect plumage development of late-hatched bluebird nestlings.

Our study provides a good estimation of the effects of hatching position on nesting condition. Late-hatched nestlings weighed less and had shorter wings than their siblings, and hatching asynchrony may jeopardize the first-year survival of late-hatched nestlings. We found few costs associated with late hatching. Indicators of extreme stress were not evident in late-hatched nestlings and, as a result, plumage ornamentation was not negatively influenced. Hatching asynchrony did not appear to be costly within this population, perhaps because Eastern Bluebirds do not show extreme variance in hatching asynchrony and brood reduction is rare. It is also possible that parents are able to compensate for potential detrimental effects on morphology and stress levels of late-hatched nestlings.

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**LITERATURE CITED**


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INNATE IMMUNE RESPONSE DEVELOPMENT IN NESTLING TREE SWALLOWS

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ABSTRACT.—We tracked the development of innate immunity in nestling Tree Swallows (Tachycineta bicolor) and compared it to that of adults using blood drawn from nestlings during days 6, 12, and 18 of the ~20-day nestling period and from adults. Innate immunity was characterized using an in vitro assay of the ability of whole blood to kill Escherichia coli. The ability of whole blood to kill E. coli increased as nestlings matured. Neither this component of innate immunity nor right wing chord length on day 18 were as developed as in adults indicating that development of the innate immune system and growth both continued after fledging. Narrow sense heritability analyses suggest that females with strong immune responses produced nestlings with strong immune responses. These data suggest nestling Tree Swallows allocated sufficient energy to support rapid growth to enable fledging by day 18, but that further development of innate immunity occurred post-fledging. Received 22 December 2010. Accepted 21 May 2011.

Ecoimmunology seeks to understand immune defense strategies observed among and within species in their natural environments (Martin et al. 2011). One area of interest is developmental ecoimmunology (Apanius 1998), which investigates how a species’ niche and life history strategy influence the rate and pattern of maturation of immune defenses (Sheldon and Verhulst 1996, Norris and Evans 2000). The strength of immune responses is generally positively correlated with yearly survival for birds (Horuk et al. 1996, Christie et al. 2001, Ardia et al. 2003, Möller and Saino 2004), but the energetic costs of activating and maintaining the immune system may negatively affect growth (e.g., Mautz et al. 2005, van der Most et al. 2011).

Young birds, after hatching, primarily use innate immune defenses if infected by a pathogen (Apanius 1998, Bar-Shira and Friedman 2006), because adaptive immune responses do not develop until exposure to foreign antigens (Roitt et al. 1998). Innate immunity, the first-line of defense, is a fast-acting nonspecific response to pathogens (Roitt et al. 1998). Young birds also depend on maternally-transferred antibodies (Hån et al. 1990, Hasselquist and Nilsson 2009) produced by their mothers in response to exposure to foreign antigens, as well as antimicrobial peptides (Ardia et al. 2011), another immune element provided in eggs. Nestling altricial birds, while confined to the nest and have bare skin before their feathers grow in and cover them, are exposed to disease organisms vectored by biting insects (Piesman and Gates 1996, Apperson et al. 2004, Ostfeld et al. 2004). They are also exposed to potential pathogens and foreign microbes (and parasites) in the food delivered to them by adults, the nest material surrounding them, and their nest mates (Kyle and Kyle 1993, Hahn et al. 2000, Lochmiller and Deerenberg 2000). Innate immune function may be especially important to altricial nestlings because: (1) their relatively short incubation periods may result in poorly developed immune systems at hatching (Rickels 1992), and (2) their lack of mobility may result in greater exposure to parasites (Ardia and Schat 2008). Altricial nestlings also have strong selection pressure to grow rapidly to fledge as soon as possible and leave the nest to avoid predation (Skutch 1976, O’Connor 1984). This suggests the rate of maturation of immune defenses reflects an evolutionary trade-off with physical growth and maturity required to fledge (Ardia and Schat 2008, Ardia et al. 2011, van der Most et al. 2011).

Assessment of maturation of immune function in wild birds has been most frequently made using a single measurement, but we monitored immune development by assaying immunocompetence throughout the nestling period (Palacios et al. 2009). We took samples at different points in the nestling period and measured one component of the innate immune response, i.e., the in vitro ability of whole blood to kill Escherichia coli, in altricial nestling Tree Swallows (Tachycineta bicolor), and compared it to adult innate immune function. We predicted the in vitro microbicidal
ability of Tree Swallow whole blood to kill *E. coli* would increase over the nesting period in synchrony with physical growth and would reach the level found in adult swallows because of its low calculated costs (Klasing 2004). Some components of innate immunity (e.g., natural antibodies, complement mediated lysis and lymphocytes) are lower in nestling Tree Swallows than in adults, but lymphocyte concentrations reach adult levels in 18-day old nestlings (Palacios et al. 2009).

We investigated the relationship between physical growth and maturation of immunity from measurements of mass and right wing chord length when we took blood samples. We assessed the heritability of the immune response by comparing the *in vitro* microbicidal ability of whole blood to kill *E. coli* in mothers and their offspring.

**METHODS**

**Study Species.**—We studied Tree Swallows that nested on the campus of Grand Valley State University in Allendale, Michigan, USA (42°57' N, 85°53' W) from May to July 2009. Our study site in a fallow agricultural field consisted of a 10 × 10 grid of 100 standard wood nest-boxes spaced 20 m apart and fitted with predator guards. Tree Swallows are primarily aerial insectivores with a socially monogamous breeding system characterized by high rates of extra-pair paternity (Robertson et al. 1992). Females usually lay clutches of 5–6 eggs that hatch after ~14 days of incubation. Hatchlings are altricial and both adults tending the nest provision nestlings until most fledge between 18 and 20 days after hatching (Robertson et al. 1992).

**Field Methods.**—We monitored nests every day to ascertain clutch completion dates, exact hatching dates, and exact nesting ages. Tree Swallow nestlings undergo three basic stages of development: their eyes open 3–4 days after hatching, they develop endothermy 8–9 days after hatching (Dunn 1979), and they fledge ~20 days after hatching (Robertson et al. 1992). We collected blood from different nestlings on nesting days (ND) 6, 12, and 18 (ND0 = the day the first egg in a clutch hatched) that are in the range of these developmental stages; nestlings were too small at ND3–4 to obtain blood samples of adequate volume to perform *in vitro* assays. Thus, due to the small size of nestlings, we obtained only a single blood sample from each individual to prevent jeopardizing its health. ND18 was the end-point measurement because some nestlings may fledge before ND20 and we wanted to ensure collecting blood samples while nestlings were available. We collected blood samples from 10 nestlings from five broods on ND6, 16 nestlings from five broods on ND12, and 22 nestlings from eight broods on ND18. We did not measure the ND6 nestlings from which we drew blood, but we did measure mass to the nearest 0.1 g on an electronic scale and flattened right wing chord to the nearest 1 mm with a ruler with a stop fixed to one end on 118 ND6 nestlings at 25 other nests at our study site. We measured nestling mass on ND12 and ND18 to the nearest 0.2 g with a spring scale and flattened right wing chord of the nestlings from which we drew blood samples.

Adult swallows were captured during the nestling phase of the breeding season using plastic box-traps (Yunick 1990). We drew blood from 79 adults (*n* = 44 females, *n* = 35 males). We measured each adult’s mass and right wing chord length. Breeding females were categorized as either second-year (SY) (*n* = 19) if the female had a mostly brown dorsal plumage, or after-second year (ASY) (*n* = 25) if the female had mostly iridescent blue-green dorsal plumage (Hussell 1983). Male Tree Swallows cannot be reliably classified to age by size or plumage characteristics (Dwight 1900, Robertson et al. 1992), but males mated to ASY females are likely to be ASY males (Robertson et al. 1992).

We drew blood (10–60 μL) from the brachial vein of swallows. The area surrounding the brachial vein was cleared of interfering feathers, soaked liberally with 70% ethanol (EtOH), swabbed with a fresh cotton ball, and allowed to air dry for 15–20 sec because EtOH can cause hemolysis, which can complicate immune assays (Millet et al. 2007). The brachial veins of nestlings and adults were punctured with either sterile 28-gauge hypodermic needles or lancets, respectively, and blood was collected in heparinized capillary tubes (50 μL capacity). Tubes were held horizontally to cause air bubble formation at the end of the tube, sealed using an EtOH-sterilized clay card, placed in sterile 50 mL test tubes, and transported to the laboratory. All blood samples were collected within 3 min of handling to avoid the effects of immunosuppression mediated by stress hormones such as corticosterone (Romero and Romero 2002). Blood was
transported to the laboratory within 60 min of collection for the best results during immune assays (Millet et al. 2007). House Sparrow (Passer domesticus) whole blood showed greater in vitro killing of E. coli (American Type Culture Collection [ATCC] #8739) than did plasma (Liehl and Martin 2009).

**Laboratory Methods.**—We followed Millet et al. (2007) to evaluate in vitro ability of whole blood to kill E. coli. The in vitro microbicidal ability of whole blood provides a measure of constitutive innate immune function (e.g., Tieleman et al. 2005, Matson et al. 2006, Millet et al. 2007) and shows individual variation and high repeatability within individuals in some bird species (Tieleman et al. 2010, Wilcoxen et al. 2010). Male Florida Scrub-Jay (Aphelocoma coerulescens) survivorship during a suspected eastern equine encephalitis epidemic was positively correlated with the in vitro ability of their whole blood to kill E. coli suggesting this measure of innate immunity may be an indicator of individual quality (Wilcoxen et al. 2010). E. coli is a potentially pathogenic Gram negative bacterium that has been isolated from the cloacae of adults (Lombarde et al. 1996) and nestlings (Mills et al. 1999), and in semen (Lombarde and Thorpe 2000) in Tree Swallows.

E. coli was supplied as 10⁷ organisms per lyophilized pellet (ATCC #8739, Microbiologies Inc., St. Cloud, MN, USA). This assay was developed to be a rapid, simple, and reliable assay to measure the effectiveness of the innate immune system to kill microbes. It integrates many of the important components of the immune system (e.g., white blood cells, natural and specific antibodies, lysozymes, and opsonins, molecules that facilitate phagocytes to identify and phagocytize microbes) (Millet et al. 2007). We also tried to use this microbicidal assay to kill Staphylococcus aureus but our attempts at this in vitro assay failed because neither adult nor nestling whole blood killed S. aureus (TS et al., unpubl. data).

All laboratory work occurred inside laminar flow hoods. Microbe pellets were reconstituted following manufacturer’s instructions in 40 mL of sterile, endotoxin-free Phosphate Buffered Saline (PBS) and held at 4° C. The stock culture was diluted with cold PBS each day that assays were run to make a working culture with ~50,000 Colony Forming Units (CFU)/mL. Working cultures were kept on ice. Whole blood was diluted 1:4 with pre-warmed (41° C) CO₂-independent media (#18045; Gibco-Invitrogen, Carlsbad, CA, USA) plus 4mM L-glutamine in a sterile 1.5 mL capped tube. Ten microliters of the working culture (=500 CFU) were added to 100 µL of diluted blood, vortexed, and incubated for 45 min at 40.5° C, samples were removed from the incubator and vortexed, and 50 µL aliquots were pipetted onto Trypticase Soy Agar (TSA) plates, spread, inverted, and incubated at 37° C for 24 hrs. Samples were run in duplicates. E. coli colonies were counted after 24 hrs. The number of CFU in the initial inoculum was calculated by working culture in media alone (i.e., 10 µL of working culture per 100 µL of media) and then immediately plated. Negative controls in which no E. coli were added were also prepared.

**Statistical Analyses.**—We calculated the mean proportion of E. coli killed (hereafter, MPK) as 1 – (mean number of experimental colonies/mean number of control colonies) following Millet et al. (2007). We calculated brood means of MPK mass, and wing chord length for use in some analyses to avoid statistical pseudoreplication. We found no significant differences between adult males and females or between SY and ASY females in the microbicidal ability of their whole blood (all P > 0.05) (BJH et al., unpubl. data), and pooled their MPK data for these analyses. We estimated narrow sense heritability by regressing midnestling MPK on midparent MPK at the seven nests for which we had nesting and adult male and female MPK data. Narrow sense heritability is the ratio of additive genetic variance to the total phenotypic variance (h² = Vₐ/Vₚ) and provides an estimate of a trait's ability to respond to selection (Lynch and Walsh 1998). Tree Swallows have a high level of extra pair paternity (Lifjeld et al. 1993, Dunn et al. 1994, Barber et al. 1996, Laskemoen et al. 2010) that can bias estimates of h² (Charmantier and Réale 2005), and we also performed a midnestling MPK-mother MPK regression at ND18 nests. Intraspecific brood parasitism is rare in Tree Swallows (Robertson et al. 1992).

Data were examined for normality and analyzed using SPSS 12.0 for Windows (SPSS 2002). We performed parametric and nonparametric analyses where appropriate. No data transformations were required. All tests were two-tailed. The probability level for significance was set at α = 0.05. Unless otherwise noted, all values are reported as mean ± SD.
RESULTS

The MPK of nestling Tree Swallow blood varied with nestling age (Kruskal-Wallis $\chi^2 = 19.48, df = 2, P < 0.001$) (Fig. 1A). The blood of only one of 10 ND6 nestlings killed *E. coli* (MPK = 0.45). The MPK of ND12 nestlings was $0.21 \pm 0.13$ ($n = 16$). The MPK of ND18 nestlings ($0.42 \pm 0.21$, $n = 22$) was less than that of adults ($0.83 \pm 0.25$, $n = 79$) (Mann-Whitney $U = 267.5, P < 0.001$) (Fig. 1A).

ND6 nestlings ($n = 118$) weighed $12.96 \pm 2.77$ g and had right wing chords of $20.63 \pm 4.06$ mm. There were no differences between ND12 ($21.13 \pm 4.05$ g, $n = 16$) and ND18 ($20.75 \pm 1.07$ g, $n = 22$) nestlings in mass ($t$-test for unequal variances, $t = 0.37$, df = 16.5, $P = 0.72$) (Fig. 1B). The wing chords of ND12 nestlings ($54.00 \pm 7.01$ mm) were shorter than those of ND18 nestlings ($83.59 \pm 4.49$ mm) (Student’s $t$-test = 15.68, df = 36, $P < 0.001$) (Fig. 1C). There were no correlations between mean brood mass or mean brood wing chord length and mean brood MPK for both ND12 and ND18 nestlings (all $P > 0.09$).

There were differences in mass (ANOVA, $F = 13.61$, df = 2.96, $P < 0.001$) among ND18 nestlings ($20.75 \pm 1.07$ g), adult females ($19.18 \pm 1.30$ g), and adult males ($19.70 \pm 0.98$ g); ND18 nestlings weighed more than adults (Bonferroni multiple post hoc comparisons, both $P < 0.01$) (Fig. 1B). Adult females and males did not differ in mass (Student’s $t$-test = $-1.95$, df = 75, $P = 0.06$).

There were differences in wing chord length (ANOVA, $F = 805.10$, df = 2.95, $P < 0.001$) among ND18 nestlings ($83.59 \pm 4.49$ mm), adult females ($113.64 \pm 3.10$ mm, $n = 44$), and adult males ($118.88 \pm 2.79$ mm, $n = 32$); the wing chords of males were longer than those of females and ND18 nestlings (Bonferroni multiple post hoc comparisons, both $P < 0.001$) (Fig. 1C).

Midnestling MPK-midparent MPK regression produced an estimate of $h^2 = 0.92 \pm 0.66$ (SE).

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**FIG. 1.** (A) Mean ± SD proportion kill (MPK) ability of whole blood to kill *E. coli* in different age classes of Tree Swallows. (B) Mean ± SD mass of different age classes of Tree Swallows, ND12 ($n = 16$), ND18 ($n = 22$), Female ($n = 44$), Male ($n = 32$). (C) Mean ± SD flattened right wing chord of different age classes of Tree Swallows, ND12 ($n = 16$), ND18 ($n = 22$), Female ($n = 44$), Male ($n = 32$).
DISCUSSION

The in vitro microbicidal ability of nestling Tree Swallow whole blood to kill *E. coli* increased during development (Fig. 1A). The in vitro microbicidal ability of whole blood is time dependent (Millett et al. 2007), and our data suggest the relative quickness of nestlings to respond to pathogens is low at ND6 and rises to about one-half of adult level at fledging (Fig. 1A). We infer from this pattern that the ability to mount an adulthood-like innate immune response in Tree Swallows requires post-fledging development.

The level of in vitro microbicidal ability of whole blood of ND18 nestlings was about one-half of adult levels (Fig. 1A) and is consistent with Palacios et al.'s (2009) findings that complement mediated cell lysis and levels of natural antibodies were not fully developed by time of fledging of Tree Swallows. In contrast, Møller and Haussy (2007) found no differences between ND12 nesting and adult Barn Swallows (*Hirundo rustica*) in complement mediated lysis. Natural antibody levels of Great Tits (*Parus major*) were fully developed by the end of the nesting period but complement activation was not detected until after fledging (DeCoster et al. 2010). Additional comparative studies of the innate immune system are needed to detect patterns of its development and the relationships between phylogeny, ecology, and innate immune responses.

The relatively slow development of the microbicidal ability of Tree Swallow nestling whole blood contrasts sharply with the rapid development of the intestinal innate immune system of precocial Domestic Chicken (*Gallus gallus*) hatchlings. Chicken hatchlings are immunologically prepared for encountering bacteria (Bar-Shira and Friedman 2006) as would be expected given their precocial condition at hatching (Ardea and Schat 2008). Comparative studies of the development of the innate immune system across the precocial and altricial spectrum in wild species should delineate differences in design and function of the immune system that reflect differences in their respective ecological niches and patterns of development (Ardea and Schat 2008).

The in vitro microbicidal ability of blood, body mass, and wing chord length all developed at different rates in nestling Tree Swallows (Fig. 1). Development of in vitro microbicidal ability of whole blood was relatively slow compared to that of body mass and wing chord length. Typically, Tree Swallow fledglings weigh about as much as adults but their wing feathers are about 80–85% of adult length (Robertson et al. 1992; Fig. 1B, C). In contrast, the in vitro microbicidal ability of their whole blood was only about one-half of adult levels (Fig. 1A). We did not detect a significant relationship between in vitro microbicidal ability of whole blood and nestling mass or wing chord length. Typically, Tree Swallow fledglings weigh about as much as adults but their wing feathers are about 80–85% of adult length (Robertson et al. 1992; Fig. 1B, C). In contrast, the in vitro microbicidal ability of their whole blood was only about one-half of adult levels (Fig. 1A). We did not detect a significant relationship between in vitro microbicidal ability of whole blood and nestling mass or wing chord length. Similarly, Palacios et al. (2009) did not find a significant correlation between nestling body condition and complement mediated cell lysis, their measure of innate immune function. The lack of relationships between MPK and Tree Swallow fledgling mass and wing chord is consistent with Morrison et al.'s (2009) finding that in vitro microbicidal ability of the plasma of ND13 Tree Swallow nestlings was not correlated with nestling body condition, as estimated by a regression of body mass on head-bill length, and hematocrit.

Our results, and those of Palacios et al. (2009), suggest the early stages of development of innate immunity in Tree Swallow nestlings may be relatively independent of body condition above a minimum threshold for healthy growth. However, a complete understanding of the relationship between development of innate immunity and nestling growth can best be evaluated by simultaneously examining several components of the innate immune system (Norris and Evans 2000).
Our results add an additional component to the full assessment of immunity (cf. Norris and Evans 2000) in nesting Tree Swallows. It is likely that components of the immune system vary in their relative costs and benefits (Klasing and Leshchinsky 1999, Evans et al. 2000, Klasing 2004), and respond differently during different life history stages (Greenman et al. 2005) and phases of development (Martin 2005).

The relative rates of development of different traits may provide clues about the possible causes of selection influencing their expression. For example, predation risk favors rapid growth and development of altricial nestlings (Skutch 1976, O’Connor 1984, Starck and Ricklefs 1998, Remes and Martin 2002). The data suggest that leaving the nest upon a predation attempt could be part of the normal behavioral repertoire of altricial nestlings (Redondo and Carranza 1989) and is associated with adaptations in nestling development (Bjorklund 1994). For example, patterns of growth in Meadow Pipit (Anthus pratensis) nestlings suggest directional selection for high growth rates; faster growing nestlings were better able to avoid predation while in the nest while slower than average growth rates placed pipit nestlings at a competitive disadvantage for food (Halpuka 1998). Post-fledging survival of slowly growing young Common Blackbirds (Turdus merula) was relatively low compared to faster growing young suggesting mortality due to lack of food and by predation were synergistic, yet both selection pressures that favor maturation of innate immune responses are likely to be stronger post-fledging than pre-fledging when causes of selection act more strongly on growth and wing development.

Our results are consistent with the view that predation risk could favor rapid growth and development at the expense of faster development of innate immunity. The in vitro microbicidal ability of whole blood in our study increased through each subsequent stage of development but adult immune potential was not reached until after fledging. The increase of in vitro microbicidal ability of whole blood to kill E. coli had no apparent effect on nesting growth and supports the hypothesis of low developmental costs of innate immunity (Klasing 2004). This supports the hypothesis that causes of selection affecting nesting Tree Swallows ultimately favor rapid growth relative to the development of the in vitro ability of whole blood to kill E. coli. This is consistent with the prediction that a negative correlation should exist between growth and development of nonspecific immune defenses (Lee 2006). For example, Mauck et al. (2005) found a negative correlation between growth and levels of immunoglobulin M (IgM), a component of the innate immune system, in nesting Leach’s Storm-Petrels (Oceanodroma leucorhoa). Experiments are required to directly test the hypothesis that an energetic trade-off exists between growth and development of innate immunity.

Midnestling MPK—midparent MPK regression estimated high heritability ($h^2 = 0.92$) of innate immunity. However, this estimate is potentially biased by extra pair paternity (50–90% of nests) (Lifjeld et al. 1993, Dunn et al. 1994, Barber et al. 1996, Laskemoen et al. 2010) which was not assessed in our study. Thus, we cannot estimate the effect of selection on the trait. We also calculated a midnestling MPK—mother MPK regression to account for this potential bias that produced a reduced estimate of heritability ($h^2 = 0.41$). This result is (1) similar to the heritability of the cell-mediated immune response to phytohaemagglutinin (PHA) injection estimated from midnestling-mother regressions of Tree Swallows in Tennessee ($h^2 = 0.42$), but not in New York or Alaska (Ardia and Rice 2006), and (2) consistent with the strong effect that nest of origin had on the ability of ND13 nestlings to kill E. coli in cross-fostering experiments in Massachusetts (Morrison et al. 2009). Similarities in heritabilities suggest similar mother genetic contributions to the cell-mediated immune response and microbicidal ability. Nest of origin influences innate immune responses, including the microbicidal ability of nestlings (Forsman et al. 2008). Nest of origin effects are likely due to both heritable and non-genetic maternal effects. For example, lysozyme, a protein that contributes to microbicidal ability, is transmitted from mothers to their nestlings via egg albumin (Board and Fuller 1974). Evidence suggests the lysozyme activity of mothers and nestlings is highly correlated (e.g., Cucco et al. 2006).

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ASSOCIATIONS BETWEEN NORTHERN MOCKINGBIRDS AND THE PARASITE *PHILOMIS PORTERI* IN RELATION TO URBANIZATION

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ABSTRACT. We investigated associations between Northern Mockingbirds (*Mimus polyglottos*) and the nest parasite *Philornis porteri* (Diptera: Muscidae), and how they vary with urbanization in northcentral Florida. Our goal was to ascertain if the ‘parasite-release’ hypothesis could contribute to high reproductive success of Northern Mockingbirds in urban areas. We collected 26 nests in 2007 and 73 in 2008 that had produced fledglings along an urbanization gradient, and measured the number of nests parasitized and the number of *P. porteri* in the nests. Habitats differed in prevalence of *Philornis* parasitism, but not directly in relation to urbanization. Parking lots and wildlife preserves had low levels of parasitism, whereas residential neighborhoods and pastures had significantly higher parasitism prevalence. Parasite prevalence was also significantly and positively affected by nest height and percentage of ground covered by buildings, trees, and open areas in the study site. Our findings do not offer strong support for the ‘parasite-release’ hypothesis in relation to urbanization, but suggest that vulnerability to parasites is habitat-specific.

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Urbanization causes high local extinction rates and replacement of many species by others that survive well in urban areas (McKinney 2002, Blair 2004, Gottschalk et al. 2007), which we refer to as urban-positive species (Stracey 2011). Numerous researchers (Adams 1994, Goring and Blair 1999, McKinney 2002, Chace and Walsh 2006, Shochut et al. 2006, Fokidis et al. 2008) have hypothesized that changes in predation and food resources are responsible for the success of urban-positive species. Few studies, however, have tested the hypothesis that urban-positive species are released from parasites that help regulate populations in native habitats. Urban species could be less exposed to parasites either because hosts are in better condition and have better immune systems to fight parasites (Fokidis et al. 2008) or because some parasites are less prevalent in urban areas (Marcogliese 2005). Some authors (Lafferty 1997, Marcogliese 2004, Sures 2004, Marcogliese 2005) suggest parasites are frequently the first species to be affected by ecosystem changes.

Parasites have an important role in structuring many ecological communities (Minchella and Scott 1991). They can regulate host populations by increasing energetic demands, altering behavior, increasing mortality, reducing fecundity, altering nutritional status, reducing growth, modifying interspecific competition, enhancing susceptibility to predation, and altering mate choice and sex ratios (reviewed by Minchella and Scott 1991). Loya and Carroll (1995) reviewed the effects of ectoparasites on birds and found they affect nestling growth, body condition, and survival, as well as adult reproductive success and behavior. They concluded that blood-feeding, nest-dwelling parasites may significantly reduce host fitness. Tompkins et al. (2011) found that parasites frequently mediate the success of invasive species. If a similar mechanism is operating in urban habitats, an additional hypothesis for high abundance of urban-positive species may be decreased parasitism.

Numerous recent studies measured the effects of urbanization on host-parasite interactions along an urban gradient (Gregoire et al. 2002, Reperant et al. 2007, Fokidis et al. 2008, Geue and Partecke 2008, Page et al. 2008, Evans et al. 2009, Lehrer et al. 2010). The frequency and the intensity of roundworm (*Baylisascaris procyonis*) infection in common raccoons (*Procyon lotor*), for example, decreased with urbanization (Page et al. 2008) and the prevalence of some species of helminth parasites in red foxes (*Vulpes vulpes*) also decreased with urbanization (Reperant et al. 2007). Similarly, for songbirds, individuals in urban areas generally had fewer blood parasites (Fokidis et al. 2008), fewer *Ixodes* ticks (Gregoire et al. 2002, Evans et al. 2009), and lower risk of infection by blood parasites (Geue and Partecke 2008) than in rural areas. Lehrer et al. (2010), however, found that prevalence of *Toxoplasma gondii* in woodchucks (*Marmota monax*) was positively related to urbanization. These studies
indicate that associations between parasites and their hosts can be either positively or negatively affected by urbanization.

Tomkins et al. (2011), in their review of the effects of wildlife diseases on ecosystems, indicate a wider exploration of the effects of parasites on invasive species' success is needed. Further studies on the distribution and effects of parasites in relation to urbanization are needed as little is known about how urbanization affects parasites and nest parasites in particular, and how these changes can affect urban bird communities.

We investigated how the interaction between the Northern Mockingbird (Mimus polyglottos) and its nest parasite (Philornis porteri; Diptera: Muscidae) varies with urbanization. Previous research (Fokidis et al. 2008, Stracey and Robinson in press) demonstrated the mockingbird, an urban-positive species, increases in abundance with urbanization with peak densities occurring in residential neighborhoods (Stracey 2010). We considered the mockingbird a model species to test if the 'parasite-release' hypothesis might contribute to the success of urban-positive species. Dipteran nest parasites are known to have deleterious effects on nestlings and, at times, adults (Arendt 1985a, b; Hurtrez-Boussès et al. 1998; Simon et al. 2004; Segura and Reboreda 2011), and assessing their presence is much less invasive than assessing blood parasites. Mockingbird nests are more likely to be infected by this parasite than by fleas or mites (pers. obs.), and Philornis is known to have negative fitness consequences including reduced growth, diminished body condition, decreased fledgling success, and increased nestling mortality for at least some hosts (Arendt 2006, Dudaniec et al. 2007, Rabuffetti and Reboreda 2007, Huber 2008, Galligan and Kleindorfer 2009). Females of most species of Philornis lay eggs in the avian hosts' nests. The larvae of subcutaneous species, after hatching, burrow under the nestlings' skin where they feed until they are ready to pupate. They then leave the nestlings, pupate in the nesting material, and emerge as adults 10 days later, allowing Philornis to produce several generations per year (Glasgow and Henson 1957, Kinsella and Winegarner 1974, Uhazy and Arendt 1986, Delannoy and Cruz 1991, Young 1993, Nores 1995, Spalding et al. 2002, Arendt 2006, Dudaniec and Kleindorfer 2006, Fessl et al. 2006). The life cycles of many Philornis parasites have been partially described, but little is known about P. porteri.

Study Sites.—Our study was conducted at seven sites in and around Gainesville, Florida, USA during spring and summer 2007 and 2008. All study sites were within 50 km of Gainesville and were spread along an urbanization gradient. These sites were grouped into four types of habitat: wildlife preserve (1 site: Ordway-Swisher Biological Station), pasture (2 sites), residential area

**METHODS**

**Study Species.**—The Northern Mockingbird is an open-cup nesting, altricial bird that occurs throughout the United States, southern Canada, Mexico, and the West Indies (Derrickson and Breitwisch 1992). The breeding season in Florida starts as early as late February and ends in early August, and a pair can nest from one to five times during the breeding season (Derrickson and Breitwisch 1992). Clutch size is between two and six eggs, and nestlings remain in the nest 12 days with both parents providing care (Derrickson and Breitwisch 1992).

*Philornis porteri* occurs in southern Texas and Florida (Dodge 1955, Kinsella and Winegarner 1974) and has been observed on at least three species of birds: Northern Mockingbirds, Eastern Bluebirds (*Sialia sialis*), and Great Crested Flycatchers (*Myiarchus crinitus*) (Kinsella and Winegarner 1974, Spalding et al. 2002). Larvae are obligate subcutaneous parasites of nestlings and feed on blood, other body fluids, and cellular debris (Dudaniec and Kleindorfer 2006, Fessl et al. 2006). Adults are non-parasitic and may feed on decaying organic matter, fruits, or flowers (Dudaniec and Kleindorfer 2006, Fessl et al. 2006). Philornis larvae are known to have negative fitness consequences including reduced growth, diminished body condition, decreased fledgling success, and increased nestling mortality for at least some hosts (Arendt 2006, Dudaniec and Kleindorfer 2006, Dudaniec et al. 2006, Rabuffetti and Reboreda 2007, Huber 2008, Galligan and Kleindorfer 2009).

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(2 sites) and parking lot (2 sites). Each site was embedded within a larger area of the same type of land use. The parking lots consisted of large areas of pavement for parking spaces, interspersed with buildings and islands of mowed grass, shrubs, or trees. The residential neighborhoods consisted of a mosaic of roads, houses, and yards. The yards had variable amounts of mowed grass and ornamental shrubs and trees that were both native and nonnative. The pastures consisted of scattered trees and large areas of grass that were periodically grazed by cattle. Fences in the pastures were often covered with vines and shrubs. The wildlife preserve consisted of scrub trees and shrubs scattered among areas of short grass and bare ground with an occasional large tree. These open areas were variably surrounded by pine (Pinus spp.) forests or xeric forests. Study sites were between 2.7 and 52.9 km apart. We calculated the percentage of ground covered by buildings, pavement, grass, open areas (sum of pavement and grass), trees, and other (water or undetermined surface) for each study site based on Google Earth satellite images. We designated wildlife preserve and pasture as rural land-use, and parking lot and residential areas as urban land-use. We only sampled nests from rural habitats in 2007. The highest densities of mockingbirds were in residential areas, followed by parking lot and wildlife preserve; pasture had the lowest densities (Stracey 2010).

Spatial Pattern of Prevalence and Intensity of Parasitism.—We searched each study site for mockingbird nests. Active nests were monitored every 1–3 days until nestlings fledged or were depredated. No botflies were detected on the nestlings during handling. We collected nests after nestlings fledged and placed them in sealed plastic bags. We only collected nests from which at least one nestling fledged to ensure that if there were parasites in the nest they had sufficient time to pupate. We also noted the date when clutches were initiated, nest height, and the type of plant containing the nest.

We dissected each nest and counted the number of pupae, pupal cases, and adult flies in the nesting material. Adult flies were identified by G. J. Steck (Florida Department of Agriculture and Consumer Services) and voucher specimens were deposited in the collection of the Florida Department of Agriculture and Consumer Services. All pupae, pupal cases, and adults were identified as *P. porteri* except a few pupal cases which belonged to a parasite (a tachinid fly) of *P. porteri*. These pupal cases were excluded from the study.

The parasite intensity in each nest was defined as the number of pupae plus the number of pupal cases in the nest. The number of nestlings in a nest varied from one to four, and we defined the average parasite intensity per nestling as the nest intensity divided by the number of nestlings at hatching day. Average parasite intensity per nestling, however, is only an estimate of parasite load because parasites may not be spread evenly among nestlings and may concentrate on one or a few nestlings (Christe et al. 1998). We calculated the proportion of parasitized nests in each site and for each year.

Statistical Analyses.—We used R Software (2010: Version 2.12.1) to test the effect of year, month in which the nest was initiated, clutch size, land-use category (urban, rural), habitat (parking lot, residential, pasture, wildlife preserve), study site, nest height, and plant type (tree, shrub, vine or building/object) on parasitism status of the nest (parasitized or not parasitized) using logistic regression. The different study sites were also defined by ground-cover variables, and we tested the effect of these variables (percentage of buildings, trees, and open areas) on parasitism status of the nest using logistic regression. We used a stepwise selection process for both models based on AIC to remove useless variables. *P* values for the effect of the different variables were obtained by performing a Type III sums-of-square analysis on the final models. We also analyzed the effect of these variables on the number of parasites per nestling for parasitized nests using ANCOVA. We log-transformed the data on parasite intensity per nestling to meet assumptions of normality. We used a stepwise selection process for both models based on AIC to remove useless variables and *P* values for the effect of the different variables were obtained by performing a Type III sums-of-square analysis on the final models.

**RESULTS**

We collected 73 nests in 2008 and 26 nests exclusively from rural areas in 2007. Thirty-eight percent of the nests were parasitized in 2008 versus 42% in 2007 (Tables 1, 2). The number of parasites in a nest ranged from 0 to 85 with a mean ± SE of 22.85 ± 3.99 parasites in the parasitized nests in 2008, and from 0 to 88 with a
mean ± SE of 22.73 ± 7.64 parasites in parasitized nests in 2007. There were many nests with few parasites in both years, and few nests with many parasites (Fig. 1A). Parasite intensity per nestling followed that same trend, ranging from 0 to 21.25 with a mean ± SE of 6.59 ± 1.15 parasites per nestling in parasitized nests in 2008 and from 0 to 88 with a mean ± SE of 14.05 ± 7.61 parasites per nestling in parasitized nests in 2007 (Fig. 1B).

Habitat had a significant effect on prevalence of parasite infestation ($\chi^2 = 10.58$, df $= 3$, $P = 0.014$). There were more nests parasitized in residential areas and pastures than in parking lots (pairwise Chi-square tests: $\chi^2 = 8.94$, df $= 1$, $P = 0.003$, and $\chi^2 = 7.04$, df $= 1$, $P = 0.008$, respectively; Fig. 2). There was a non-significant trend for more parasitized nests in residential areas than in the wildlife preserve ($\chi^2 = 2.73$, df $= 1$, $P = 0.098$; Fig. 2). Nest height also had a positive effect on the probability of being infected ($\chi^2 = 4.52$, df $= 1$, $P = 0.033$). There was a trend ($\chi^2 = 3.58$, df $= 1$, $P = 0.058$) for nests later in the year to have a higher probability of parasitism.

### Table 1: Characteristics of parasite prevalence, parasite intensity, parasite intensity per nestling, and clutch size of Northern Mockingbirds at each site during the 2007 breeding season, Gainesville, Florida. ORD = Ordway-Swisher Biological Station, BRU = Beef Research Unit, and SF = Santa Fe River Ranch Beef Unit.

<table>
<thead>
<tr>
<th>Land-use</th>
<th>Rural</th>
<th>Preserve</th>
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<th>Pastures</th>
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<td>11</td>
<td>6</td>
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<tr>
<td>Prevalence</td>
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<tr>
<td>Mean intensity</td>
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<td>28.25</td>
<td>11.00</td>
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<tr>
<td>Standard error</td>
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<td>20.35</td>
<td>6.51</td>
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<td></td>
</tr>
<tr>
<td>Range</td>
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<td>4-24</td>
<td></td>
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<tr>
<td>Mean intensity/nestling</td>
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<td>24.08</td>
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<tr>
<td>Standard error</td>
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<td>21.35</td>
<td>2.05</td>
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</tr>
<tr>
<td>Range</td>
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<td>2.91</td>
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</table>

Table 2: Characteristics of parasite prevalence, parasite intensity, parasite intensity per nestling, and clutch size of Northern Mockingbirds at each site during the 2008 breeding season, Gainesville, Florida. ORD = Ordway-Swisher Biological Station, BRU = Beef Research Unit, SF = Santa Fe River Ranch Beef Unit, DUCK = Duckpond, CAPRI = Capri, OM = Oaks Mall, and BP = Butler Plaza.

<table>
<thead>
<tr>
<th>Land-use</th>
<th>Rural</th>
<th>Preserve</th>
<th>BRU</th>
<th>Pastures</th>
<th>SF</th>
<th>Residential areas</th>
<th>Urban</th>
<th>Parking lots</th>
</tr>
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<tbody>
<tr>
<td>Sample size</td>
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<td>7</td>
<td>13</td>
<td></td>
<td></td>
<td>10</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>Prevalence</td>
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<td>0.43</td>
<td>0.69</td>
<td></td>
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<td>0.70</td>
<td>0.57</td>
<td>0.18</td>
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<tr>
<td>Mean intensity</td>
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<td>49.67</td>
<td>22.89</td>
<td></td>
<td></td>
<td>17.29</td>
<td>23.50</td>
<td>19.50</td>
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<tr>
<td>Standard error</td>
<td>3.00</td>
<td>18.59</td>
<td>6.19</td>
<td></td>
<td></td>
<td>7.10</td>
<td>9.63</td>
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</tr>
<tr>
<td>Range</td>
<td>1-7</td>
<td>22-85</td>
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<td>1-52</td>
<td>1-41</td>
<td>19-20</td>
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<tr>
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<td>Range</td>
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FIG. 1. Number of Northern Mockingbird nests collected in 2007 and 2008 according to (A) their number of parasites and (B) number of parasites per nestling (total number of parasites divided by number of nestlings in the nest).
Habitat

Proportion of parasitized Northern Mockingbird nests in each habitat. WP = wildlife preserve, PAST = pasture, RES = residential, and PL = parking lot. Asterisks show habitats with significantly different parasite prevalence. WP and RES were significantly different at the 10% level but not 5%.

DISCUSSION

The prevalence of *P. porteri* differed among habitats with fewer parasitism in nests in the wildlife preserve and parking lots than in pastures and residential areas (Fig. 2). This result was not consistent with the parasite-release hypothesis which indicates parasitism would decrease with urbanization. The percentages of buildings, trees, and open areas positively affected the probability of being parasitized. The relationship among these three parameters and urbanization, however, is not straightforward and their interactions could explain the observed habitat effects. The percentage of ground covered by buildings increases with urbanization, but the percentage of ground covered by trees tends to decrease with urbanization. The percentage of open areas does not seem to be correlated with urbanization as it is lowest in residential areas and highest in pastures (Table 3). Little is known about the life cycle of *P. porteri* and it is difficult to explain the pattern of higher prevalence of parasitism at moderate levels of urbanization. It could be tied to abundance of food resources for adult flies, presence of predators of adult flies including their parasites, distance between nests, or other mechanisms. We detected at least one parasite of *P. porteri* (a tachinid fly found at the wildlife preserve), but we know nothing of the abundance of this parasite or even the identity of potential predators of adult flies.

The abundance of the host could also influence the prevalence of parasitism by providing more or fewer nests in which the parasites can lay eggs. High densities of hosts could result in a dilution effect (Ostefeld and Keesing 2000), i.e., a lower proportion of mockingbird nests being parasitized. Fewer hosts would result in a higher proportion of nests being parasitized. Our results, however, showed little relationship between host density and parasite prevalence as the highest parasite prevalence was in habitats with both high

<table>
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<tr>
<th>Land-use Habitats</th>
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<th>Residential Areas</th>
<th>Urban</th>
<th>Parking Lots</th>
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<td>Trees</td>
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<td>79.60</td>
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<td>0.24</td>
<td>0.95</td>
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TABLE 3. Percentage of ground covered by buildings, open areas (sum of pavement and grass), trees, and other (water or undetermined surface) calculated for each Northern Mockingbird study site from satellite images, Gainesville, Florida, 2007-2008. ORD = Ordway-Swisher Biological Station, BRU = Beef Research Unit, SF = Santa Fe River Ranch Beef Unit, DUCK = Duckpond, CAPRI = Capri, OM = Oaks Mall, and BP = Butler Plaza.
(residential) and low (pastures) host densities. We did not consider other hosts of *P. porteri*, which might affect host-specific parasitism rates (Ostfeld and Keesing 2000). Kleindorfer and Dudaniec (2009), for example, found that parasite intensity was significantly higher for nests with many close heterospecific neighbors in a related species of botfly. *P. porteri* has been documented in nests of two other species: Eastern Bluebirds (Spalding et al. 2002) and Great Crested Flycatchers (Kinsella and Winegarner 1974, Spalding et al. 2002), both of which occurred in wildlife preserves, pastures, and residential areas, but were uncommon in parking lots (CMS, unpubl. data). We do not have data on parasitism rates of these species, nor do we know if additional species also serve as hosts.

It is unclear if urbanization affects the distribution of *P. porteri*. This parasite may benefit from changes caused by moderate levels of human land modification, such as in pastures and residential areas. Residential areas in Gainesville still contain native vegetation and are characterized by moderate percentages of ground covered by buildings (7.06 and 28.49% at our study sites) and pavement (5.80 and 19.44% at our study sites, Table 3). This pattern has also been documented for the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, which reaches highest abundance at moderate levels of urbanization (Chace et al. 2003), although undoubtedly for different reasons. Our findings offer weak support, at best, that the 'parasite-release' hypothesis could explain why urban-positive species like mockingbirds are so successful in urban areas. Only the most extreme urban environments appear to offer a refuge from botflies and birds nesting in habitat with the most natural vegetation also had a refuge from high levels of botfly parasitism. Our results are difficult to interpret without a more complete understanding of the ecological factors that affect the distribution of *P. porteri*. The importance of *P. porteri* selective pressure on mockingbirds relative to other parasities and other factors (i.e., food and predators) is unknown. Our study highlights the limitations in our understanding of how urbanization affects bird communities through its effects on parasities. Given the potential of parasities to have an important ecological role in structuring bird communities, continued research into the affects of urbanization on parasities is vital.

**ACKNOWLEDGMENTS**

We thank G. J. Steck for identifying the parasite, Judi Ungvari-Martin for assistance with nest dissection, and Steve Daniels, T. J. Richard, and R. E. Hamauer for help with field work. We thank Butler Plaza, the Oaks Mall, the University of Florida Beef Research Units, Odway-Swisher Biological Station, and all homeowners who granted permission to work on their properties.

**LITERATURE CITED**


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STRACEY, C. M. 2010. Pattern and process in urban bird communities: what makes the Northern Mockingbird


SEASONAL DISTRIBUTION AND RANGE OF THE BLACKISH-BLUE SEEDEATER (AMAUROSPIZA MOESTA): A BAMBOO-ASSOCIATED BIRD

LEONARDO ESTEVES LOPES,1,4 JOÃO BATISTA DE PINHO,2 AND CARLOS EDUARDO R. T. BENFICA3

ABSTRACT.—Avian bamboo specialists are an ecologically distinctive group of birds in the Neotropics with some seedeater species having nomadic movements following bamboo (Guadua, Chusquea or Rhipidocladum) mast seeding. We reviewed the range and seasonal distribution of Blackish-blue Seedeaters (Amaurospiza moestae) using published and unpublished records, museum specimens, sound libraries, and intensive field work. We report the first occurrence of Blackish-blue Seedeaters in the Brazilian State of Mato Grosso, a male collected in Fazenda Baja de Pedra, Cáceres (16° 27' 29" S, 58° 09' 59" W). We also recorded this species in two localities in the Cerrado region (a tropical savannah) of Minas Gerais: the Santo Antonio River, Presidente Olegário (18° 07' 48" S, 46° 11' 57" W), and the Abaete River, São Gonçalo do Abaeté (18° 05' S, 45° 22' W). These records represent a remarkable range extension, demonstrating this species is distributed across the Cerrado. We found no evidence of regular large scale or local movements of this species, which seems to be resident, at least in Argentina, which had the largest data set. Received 15 September 2010. Accepted 4 April 2011.

Amaurospiza is a small and homogeneous neotropical genus of mid-size finches generally associated with bamboo (Guadua, Chusquea or Rhipidocladum) thickets and dense forest undergrowth (Ridgely and Tudor 1989, Stotz et al. 1996, Lentino and Restall 2003). Avian bamboo specialists generally have two distinct life-history strategies. The first is exhibited by insectivorous resident species that inhabit forests dominated by bamboo, where they find shelter, nest sites, and food (Parker et al. 1997, Areta et al. 2009). The second is specialization on bamboo seeds, which is a rarer strategy, because these specialists must rely on an ephemeral source of food (Areta et al. 2009). This is because most woody bamboo species are semelparous (individuals have only a single period of reproduction in their lives, after which they die) with simultaneous flowering and subsequent death of entire populations that, in certain American bamboos, occur in cycles of 30–40 years (Janzen 1976, Judzicu'icz et al. 1999, Bysiriakova et al. 2004). Bamboo seed specialists, therefore, wander to survive, and nomadic move-

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been investigated in detail, and it has been suggested that all *Amaurospiza* are nomadic to some extent (Lentino and Restall 2003). The Blackish-blue Seedeater feeds mainly on seeds, but it does not appear to be an obligatory specialist on bamboo seeds (Areta et al. 2009); consequently, it may not need to wander to survive. Records of this species in extreme southern Brazil are concentrated in some months of the year (Belton 1994) and the possibility that it performs regular seasonal migration has not been investigated. We reviewed the range of the Blackish-blue Seedeater and present noteworthy range extensions. We studied its seasonal distribution, looking for evidence of regular large scale movements in latitude, longitude, or elevation. The possibility of nomadic movements by this species was also briefly considered.

**METHODS**

Several sources of data were used to identify the range of Blackish-blue Seedeaters. We (1) compiled our unpublished field records and those obtained by several experienced observers; (2) performed wide literature review; (3) visited nine Brazilian and three North American museums; (4) wrote to curators of another four Brazilian and five European museums; (5) checked the on-line data bases of many other museums, and (6) checked for tape recordings in three sound libraries. Geographical coordinates were obtained from ornithological gazetteers (Paynter 1989, 1995; Paynter and Traylor 1991). We also benefited from a wide review by L. P. Gonzaga when he sketched an account of this species for the American birds Red Data Book (Collar et al. 1992), which was later not included.

We examined the seasonal distribution of this species from three bivariate plots with the month along the x-axis and latitude, longitude, and elevation along the y-axis. Seasonal concentration of records in some areas of the plot should provide evidence for regular long-distance or altitudinal migration.

Small scale or nomadic movements are more difficult to study, requiring long-term bird monitoring programs, which are lacking for Blackish-blue Seedeaters. Evidence of local fluctuations in abundance of this species can be obtained by examining the monthly variation in number of collected specimens in the Province of Misiones, Argentina, which has the largest series of this species. We are aware these data are sensitive to bias in collecting effort. We circumvented this problem by making comparisons between the number of Blackish-blue Seedeaters and Buff-fronted Foliage-gleaners (*Philydor rufum*) collected throughout the year. This latter is a forest species (Remsen 2003) that also inhabits areas with extensive growth of bamboo (Rodrigues et al. 1994). We used Spearman Rank Order Correlation (Sokal and Rohlf 1995) to investigate if numbers of collected specimens of both species were correlated. A strong correlation should suggest that monthly variation in the abundance of Blackish-blue Seedeaters is attributable to collecting effort and that, consequently, it is a resident species, as is the Buff-fronted Foliage-gleaner.

**RESULTS AND DISCUSSION**

Blackish-blue Seedeaters range from southeastern Brazil (eastern Minas Gerais and Rio de Janeiro southward) to southeastern Paraguay and northeastern Argentina in the Atlantic Forest (Fig. 1); a complete list of the occurrences of this species, including unacceptable records is available upon request from the senior author). It also occurs in the Cerrado region in the states of Maranhão (Hellmayr 1929), Tocantins (Pacheco et al. 2007), and Mato Grosso do Sul (Silva 1995b). We present the first records for the Cerrado from Minas Gerais and the first state record for Mato Grosso.

The first Minas Gerais record was obtained in the Santo Antônio River (18° 07' 48" S, 46° 11' 57" W, 680 m asl), municipality of Presidente Olegário. A single male was observed singing on 2 March 2009 and a female was mist-netted the following day. Both individuals were photographed. Local vegetation was a second growth riparian forest (4—9 m tall) with dense understory dominated by an unidentified bamboo species bearing seeds. A second record was obtained on 22 October 2010 by Eduardo Gazzinelli (pers. comm.) on the Abaeté River (18° 05' S, 45° 22' W, 635 m asl), municipality of São Gonçalo do Abaeté (tape-record deposited in XC 67339, acronyms in Table 1). These localities are <90 km apart.

The Mato Grosso record was obtained on 24 February 2008, when we tape-recorded (ASEC 16382 and XC 21052) the typical song of this species in the Fazenda Baía de Pedra (16° 27' 29" S, 58° 09' 59" W, 110 m asl), municipality of Cáceres (Fig. 1). This area is in the northern
The range of the Blackish-blue Seedeater (*Amaurospiza moesta*). Black dots indicate occurrences in the Atlantic Forest and white boxes with dots indicate occurrences in the Cerrado: 1 = Tranqueira (Hellmayr 1929), 2 = Fazenda Harmonia (Silva 1995b), 3 = Lizarda, 4 = Santa Maria do Tocantins, 5 = Miracema do Tocantins (Pacheco et al. 2007), 6 = Fazenda Baía de Pedra (this study), 7 = Santo Antonio River (this study), and 8 = Abaeté River (this study). Gray tones indicate the main vegetation types (Olson et al. 2001).
Table 1. Acronyms of institutions visited or consulted and location.

<table>
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<tr>
<th>Acronym</th>
<th>Institution</th>
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<tr>
<td>AMNH</td>
<td>American Museum of Natural History</td>
<td>New York, NY, USA</td>
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<td>ZMB</td>
<td>Museum für Naturkunde</td>
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Pastures and rice plantations (Luciano Arruda, pers. comm.). The area was abandoned ~25 years ago, and is now covered by a dense stand of 3-m tall Guadua bamboo, a common invasive species in the region. This same bamboo stand produced fruits in 2007, accordingly to local owners, but we did not observe seeds when we visited the area.

The range of Blackish-blue Seedeaters is puzzling with scattered occurrences in regions subject to several different climatic regimes, elevation, and vegetation types. This species appears to be absent or rare in extensive areas of apparently suitable habitat in southeastern Brazil. The patchy distribution of Blackish-blue Seedeaters across the Cerrado may also be due to sampling effort, because ~70% of it has not been satisfactorily sampled for birds (Silva 1995a). Particularly poorly sampled is the central-north and western portion, where extensive areas dominated by Guadua woody bamboos occur (Bystrakova et al. 2004: map 3.4). These regions are poorly sampled as demonstrated by several first reports of Kaempfer’s Woodpecker (Celeus obrienii), a bamboo specialist, until quite recently known only from its type specimen collected in 1926 (Dornas et al. 2011).

The Blackish-blue Seedeater seems to be common in its limited range in Argentina (Chebez 2009). William Partridge collected more than 130 Blackish-blue Seedeaters in Misiones in the 1950s (Partridge 1953, 1954). In contrast we located <50 skins of this specimen from throughout its range outside Misiones.

We found no evidence of regular large scale movements in latitude, longitude or elevation by this species, as demonstrated by three bivariate
ACKNOWLEDGMENTS

LEL benefited from a doctoral fellowship from FAPE-MG during part of this study. Our field work was supported by grants from Núcleo de Estudos Ecólogicos do Pantanal, Centro de Pesquisa do Pantanal, Instituto Nacional de Áreas Unidas, and Ministério da Ciência e Tecnologia. Visits to North American museums were made possible through a Collection Study Grant received by LEL from AMNH. Luciano Arruda allowed our study in Cuiabá. We are grateful for logistic support. Pedro Viana kindly identified specimens collected in Misiones through the year are probably attributable to collecting efforts, as demonstrated by the positive correlation between numbers of collected specimens of Buff-fronted Foliage-gleaners and Blackish-blue Seedeaters (Spearman Rank Order Correlation; n = 12, R = 0.63, P = 0.03). Data available for Brazil are scarce, and does not allow a similar analysis. However, in the State of Paraná, which provides the majority of Brazilian records, there are records for all months of the year, except December. We cannot reject the hypothesis of nomadic movements with the data available, but we found no evidence of regular large scale or local movements, suggesting this species is a year-round resident, at least in Argentina.

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STORNS Olson and Brian Schmidt (USNM). The following curators kindly sent data on specimens housed in their collections: Roberto Rodrigues (UFPE), Pedro Scherer Neto (MNHC), Carla Fontana (MCN-PUCRS), Glayson Beoncke (MCN-FZB), Ernst Bamberg (NMW), Göran Frisk (NRM), Sylke Frahnert (ZMB), Karl Ludwig Schuchmann (ZFMK), and Robert Frys-Jones (NHM). The following museums kindly made available online data on specimens housed in their collections at the Specieslink (http://splink.criis.org.br) or at the ORNIS (http://ornisnet.org) portals: LACM, UMZC, FMNH, and IAL. Luiz Gonzaga sent data on tape recordings deposited in the sound archive under his care (ASEC), as well as a compilation of records of this species. XC (http://wwww.xeno-canto.org) and ML (http://macaulaylibrary.org/index.do) kindly made available online their sound archives. C. E. Braun, Peter Vickery, Gary Richison, Robin Restall, Juan Areta, Marcelo Vasconcelos, and an anonymous reviewer provided useful comments on previous versions of this manuscript.
Seasonal Movements and Environmental Triggers to Fall Migration of Sage Sparrows

Kurt A. Fesenmyer\textsuperscript{1,2} and Steven T. Knick\textsuperscript{1,3}

ABSTRACT.—Post-breeding ecology of shrubland passerines prior to onset of migration is unknown relative to dynamics of breeding areas. We radio-marked and monitored 38 Sage Sparrows (Amphispiza belli ssp. nevadensis) at one site in Oregon and two in Nevada from September to mid-November 2007 to track local movements, estimate seasonal range sizes, and characterize weather patterns triggering onset of migration. Median area used by Sage Sparrows monitored between 3 and 18 days during or prior to migration was 14 ha; maximum daily movement was 15 km. Radio-marked Sage Sparrows at each location departed individually, rather than en masse, corresponding with passage of cold front weather systems. Conventional telemetry techniques limited our ability to monitor Sage Sparrows beyond pre-migratory periods and precluded detecting and tracking actual movements during migration.

METHODS

We surveyed 18 randomly-selected 1-km transects in shrublands of the northern Great Basin during early September 2007 to identify regions and general habitats used by pre-migratory Sage Sparrows. Transects were within contiguous patches of uniform habitat types based on existing vegetation type classifications (LANDFIRE 2006). We assessed habitats varying in productivity and disturbance that ranged from cheatgrass (Bromus tectorum) grasslands at low elevations to low-density pinyon (Pinus spp.) and juniper (Juniperus spp.) woodlands at upper elevations of shrubland distributions. We observed Sage Sparrows on only six transects, including three in Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) and three in black greasewood (Sarcobatus vermiculatus). Greatest concentrations of Sage Sparrows occurred in locally productive shrublands (i.e., those with greener foliage and higher seed production) dominated by greasewood along alluvial draws and adjacent to playas.

We used these gross characteristics to select three study sites within north-south-oriented valleys: Pueblo Valley, Oregon (42° 00' N, 118° 36' W; 7 to 24 Sep); Silver State Valley, Nevada (41° 21' N, 117° 53' W; 3 to 26 Oct); and Carson Sink, Nevada (39° 54' N, 118° 14' W; 27 Oct to 10 Nov). We hypothesized that north-south-
oriented valleys of the Basin and Range province would facilitate ground-based tracking using conventional telemetry methods. Study site locations and sampling periods were staggered with work occurring at the most northern site in September and at the most southern site in late October. Study sites were in the southwestern portion of the breeding range of *Amphispiza belli* ssp. *nevadensis* (Johnson and Marten 1992). Sage sparrows from these areas generally depart on migration from mid-September to mid-November (Littlefield 1990).

Predominant vegetation at all sites was black greasewood; salt desert shrubs (*Atriplex* spp.) and Wyoming big sagebrush comprised minor portions of shrub communities. Sage Sparrows were observed eating greasewood seeds and many individuals captured for marking had inkweed (*Suaeda* spp.) stains on their bills. Inkweed has been associated with Sage Sparrows in wintering areas (Meents et al. 1982).

We captured Sage Sparrows by flushing them into mist nets and use of audio playbacks, classified birds as adults (AHY) or hatch year (HY), and attached 0.55-g transmitters (Advanced Telemetry Systems Inc., Isanti, MN, USA) using a figure-8 harness (Rappole and Tipton 1991). Transmitters were ~3.0% of bird mass and were below the recommended maximum of 5% (Cac- camise and Hedin 1985). We monitored presence of birds and triangulated at least one location daily from 0630 to 1900 hrs MST using hand-held Yagi antennae. Up to three birds were monitored each night by placing data-logging receivers (Lotek Wireless Inc., Newmarket, ON, Canada) and Yagi antennae in their immediate (<100 m) vicinity at dusk.

We recorded Global Positioning System coordinates of observer, time of observation, and compass bearing for each telemetry location. We estimated point locations of birds using maximum likelihood methods and 95% confidence interval error ellipses (LOAS 4.0, 3.1; Ecological Software Solutions LLC 2004). We calculated a minimum convex polygon (MCP) for each bird after discarding triangulations with error ellipse axes >250 m or biangulations (bird locations based on 2 telemetry points) outside the MCP of all other observations for each individual. Point locations and MCPs were imported into a Geographic Information System (ArcGIS 9.2; ESRI Inc., 2008) for additional mapping, including area calculations and daily movement statistics based on distance between daily sequential observations. We characterized Sage Sparrows as having migrated if they were not located after 2 days within a 35-km search radius.

We obtained weather data from the nearest weather station (Pueblo Valley barometric pressure = KREO, 121 km; Pueblo Valley all other measurements = FLS03, 46 km; Silver State Valley = KWMC, 48 km; Carson Sink = CSNSK, 18 km) compiled in the MesoWest data archive (Horel 2007). Hourly measurements were summarized to daily mean, maximum, and minimum temperatures, mean relative humidity, mean barometric pressure (Pressure Mean Sea Level, corrected for elevation), and mean wind speed. Wind direction data were retained in an hourly format. We used principal component analysis (PCA) and factor loadings to characterize weather conditions of days when we lost radio contact with any bird and for 1-2 days before and after the assumed departure day.

**RESULTS**

We radiomarked 38 Sage Sparrows (Pueblo Valley = 2 AHY, 3 HY; Silver State Valley = 4 AHY, 8 HY; Carson Sink = 5 AHY, 16 HY). We recorded 477 bird locations of which 455 were retained: 380 based on triangulations, 68 biangulations, and 7 single observations when a bird was observed. Mean number of total observations per bird was 13.5 (range = 1—39) and mean number of daily observations was 1.7 (range = 1-6). Our longest tracking period for an individual spanned 18 days. Mean transmitter/receiver distance was 266.5 m; we were able to detect signals at distances up to 1.5 km when listening from local high terrain. Mean observation error (mean length of max and min error ellipse axes) for retained locations was 42.9 m (range = 0—235 m).

Three radio-marked birds died during the study; two (1 AHY and 1 HY) appeared to have been preyed upon by raptors. A radio transmitter from one HY was recovered within a regurgitated pellet consistent in size with those produced by Short-eared Owls (*Asio flammeus*) or Northern Harriers (*Circus cyaneus*) (C. D. Marti, pers. comm.), both species were observed regularly during the study. A third HY died from an unknown cause.

**Range Size and Movements.—** We calculated range sizes for 35 of 38 marked Sage Sparrows after filtering data to remove individuals with <3 days of observation or <5 triangulated locations. Typical daily movements were <1 km
across all sites; median area used by individuals was 14.0 ha (range = 1.3–1.436 ha) during observation periods ranging from 3 to 18 days and there was no relationship between days of observation and range size ($r^2 = 0.04$). Median area used increased as the migratory season progressed (Pueblo Valley = 3.9 ha; Silver State Valley = 16.8 ha; Carson Sink = 17.6 ha) (Fig. 1); median area used was greater among HY (17.5 ha) than AHY birds (9.7 ha) across all sites.

One bird at the Carson Sink site used an area >1.400 ha during 10 days of observation. This bird was captured on 29 October, and by 6 November had moved 11 km south of its capture location. On the morning of 7 November, the bird moved 7.8 km farther south, only to return 7.8 km north by the afternoon to finish the day within 100 m of where it had roosted the day prior. The bird moved no more than 500 m from the area over the next 3 days.

Migration Departures.—Eighteen of 38 radio-marked birds departed the study site during our observation period. We did not include one bird that departed within 2 days of capture because of possible stress-induced behavior or because it may have been an itinerant migrant. Only one bird departed during 165 bird-nights (35 individual birds monitored during 55 nights) of night-time observation with data-logging receivers; time of departure was –2 min prior to end of civil twilight. All other departures occurred at unknown times on 10 days during the period 7 September to 9 November; the first departure was on 13 October and last on 9 November. Five of 18 departures occurred on one day (18 Oct).

The first three PCA axes explained 87% of the variation in the variables describing weather conditions on the 10 days that birds departed from study areas (Table 1). The first principal component represented warmer, windier, and
lower pressure conditions during the days preceding departure. The second principal component corresponded to increased temperature and wind 24 hrs after departure. The third PCA axis was characterized by increasing pressure and calming winds 48 hrs after departure.

**DISCUSSION**

Fall range sizes during or prior to migration of radio-marked birds in our study were substantially larger than territory sizes of breeding Sage Sparrows (2 ha; Wiens et al. 1985, Misenhelter and Rotenberry 2000, Vander Haegan et al. 2000), implying that resource use or availability or exploratory movements differ across seasons. The increasing amount of area used by birds as the season progressed (Pueblo Valley [Sep] vs. Silver State Valley [Oct] and Carson Sink [late Oct and Nov]) may reflect pre-migratory movements or variability in habitat quality among sites or within seasons. We were unable to follow any Carson Sink birds beyond 15 days due to study logistics; large distances moved by non-migratory birds at this site may represent pre-migratory movements for departures after our study concluded.

Sage Sparrows did not exhibit gradual movements south as we had anticipated. Rather, birds departed and were not subsequently located by conventional telemetry techniques. We made a key assumption that birds not relocated within 35 km had truly departed. Given that one bird made a daily movement >15 km, other birds also may have made similar movements that went undetected, although we continued to listen for signals from these birds at the study site and surrounding region. We were unable to distinguish radio-marked birds as residents that had bred or were reared in the immediate vicinity, or as migrants from farther north using sites as stopover habitats.

The PCA axes indicated passage of cold front weather systems during the day or evening prior to assumed departure day. The transition from a warm, windy, low pressure period to a cooler, calmer, higher pressure period triggered departures of marked birds from our study sites. This pattern is well-described for fall migrants in central and eastern North America (Hassler et al. 1963, Able 1972, Allen et al. 1996, Calver et al. 2009), but has not previously been reported for shrubstepe passerines of the intermountain region. Most birds were not under observation...
when they departed and night-time departures were almost nonexistent within the subset of birds monitored each evening. Departure just prior to the onset of civil sunset by one Sage Sparrow was consistent with migration-timing studies of other nocturnally-migrating species (Cochran 1987).

ACKNOWLEDGMENTS

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Nesting of the Pectoral Sparrow (Arremon taciturnus) in Southeastern Peru

Simon O. Valdez-Juarez1−4 and Gustavo A. Londoño2

ABSTRACT.—We report the first detailed account of the breeding biology of the Pectoral Sparrow (Arremon taciturnus). We found 15 dome nests, each containing two eggs in a spherical interior chamber. Eggs were variable in color, ranging from immaculate glossy white to white heavily spotted with brown. Incubation patterns were obtained for six nests for time spans that ranged from 1 to 15 days for a total of 28 days across nests. Incubation in all nests was solely by the female, spending an average of 51% (range 20–65%) of daylight incubating, leaving the nest an average of 7.4 times per day (range = 4–7) with an average trip length of 46.4 min (range = 6–263 min.). Nest temperature averaged 29.2 ± 2.64 C when the female was incubating and decreased to 26.6 ± 2.43 C during incubation recess. Eggs in only two nests hatched and were monitored for 2 and 9 days. The male provided the young with 75% of the food. Nestlings gained an average of 2.53 g per day. Incubation, provisioning behavior, and egg coloration were similar to other species of Arremon; however, nest shape, location, and materials differ among species. Received 17 January 2011. Accepted 3 June 2011.

The genus Arremon is composed of 10 species, eight of which have published nest descriptions (Skutch 1954, Haverschmidt 1968, Tye and Tye 1992, Auer et al. 2007); four only have information about incubation and chick-rearing behavior (Skutch 1954, Martin 2002). The Pectoral Sparrow (Arremon taciturnus) is common throughout the Amazon rainforest from the eastern base of the Andes in Colombia, Brazil, Bolivia, and Peru to most of the Amazon rainforest in Venezuela, Guyana, Suriname, and Argentina (Hilly and Brown 1986). It is common and widely distributed, but little is known about its nesting biology with most of the information generated by sporadic observations (Snethlage 1935, Haverschmidt 1968).

Detailed nesting biology descriptions are fundamental to understanding variation in avian reproductive strategies, which can improve our understanding of the geographic diversity of avian reproductive traits and life history strategies (Auer et al. 2007). Nests and behaviors are useful to reconstruct phylogenetic relationships (Zyskowski and Prum 1999), and filling gaps in current knowledge becomes relevant, especially since the number of species in the genus Arremon is still being debated (Cadena and Cuervo 2010). Our objective was to provide detailed observations of the nesting biology of Arremon taciturnus, and to compare it with the available information for this and other species of the genus.

METHODS

Study Area.—This study was conducted in the foothills of Manu National Park, Cusco, Peru near the Tono River (12° 57’58.2" S; 71° 34’ 05.3" W). The average annual temperature for the location is 24.4 °C (range = 19.3–30.7 °C). We searched for nests 6 days a week from 0600 to 1700 hrs (local standard time) between mid-August to mid-December in 2008 and 2009 covering 2 km² of forest at elevations between 800 and 1,100 m.

Nest and Eggs.—Once a nest was found, eggs were weighed to the nearest 0.05 g with a digital pocket scale (FlipScale F2: My Weigh Inc., Kelowna, BC, Canada; http://www.myweigh.com) and measured to the nearest 0.1 mm with callipers. Two to three temperature sensors were placed in six of the nests. The first sensor was placed inside the nest directly under the eggs. A second sensor was placed outside the nest to record ambient temperature. An additional temperature sensor was placed inside a fresh egg in one of the nests; the sensor was introduced by drilling a small hole in the shell, and sealing it with super glue after the sensor had been added. All sensors measured temperature every minute and the information was stored on a U12 4-channel hobo data logger (Onset Computer Corporation, Pocas-
set. MA, USA; http://www.onsetcomp.com). This allowed reconstruction of the temperatures experienced by the embryo, the nest microclimate, and the time at which the parent left or returned to the nest, the latter indicated by temperature shifts of at least 1.5 °C. The information contained in the data logger was downloaded every 10 days until the eggs hatched, or when the nest was no longer active due to predation or abandonment.

Provisioning Behavior and Nestling Growth.—The sensors were removed in the two nests where eggs hatched and the chicks were weighed daily to the nearest 0.05 g. Provisioning behavior was recorded by a motion sensor-triggered camera (CO85 Rapidfire Professional: Reconyx Inc., Holmen, WI, USA) placed between 0.5 and 0.7 m from the nest entrance. We activated the camera to take 12 photographs with any movement between the nest entrance and the camera. Pectoral Sparrows are sexually dimorphic and it was possible to record differences in provisioning behavior by gender.

Data Analysis.—Incubation rhythm was analyzed following Londono (2009). The algorithm used detected all intervals when temperature changed monotonically and three values were retrieved for each interval: duration, total decrease/increase in temperature, and initial rate of temperature increase/decrease. The start of an in-bout or off-bout period was triggered when temperature increased or decreased, respectively, at an initial rate of at least 0.5 °C/min (Cooper and Mills 2005).

RESULTS

We found four nests in 2008 and 11 in 2009; most were found when one of the parents flushed. Incubation patterns were obtained in six nests for time spans that ranged from 1 to 15 days depending on how long the nest was active, for a total across all nests of 28 incubation days. Only two nests produced nestlings and were monitored for 2 and 9 days, respectively before all young were predated.

Nest and Eggs.—Nests had a bulky rooted cup with a side entrance and a spherical interior chamber. Fourteen nests were found <0.2 m above ground level on gentle slopes with poor drainage. Nest sites were usually within the vicinity of a stream, where the soil was saturated with water. The entrance of the nest faced down slope with the back of the nest against a live tree, a fallen log, or the slope. The only nest not found in these conditions was on a shallow shelf formed naturally in the bark of a live tree, ~1 m above ground level.

Average (± SD) external nest dimensions were 121.1 ± 27.3 × 132.8 ± 19.6 mm in length and width, and 124.8 ± 32.2 mm in height (n = 10). The nest entrance averaged 56.5 ± 25.8 mm in width × 75.7 ± 11.9 mm in height (n = 10). Internal distance from the entrance to the back wall of the chamber averaged 72.8 ± 14.0 mm (n = 10) with an average inner cup depth (where eggs were deposited) of 56.5 ± 25.8 mm (n = 10). We collected and weighed nests after they were no longer active; the average fresh nest mass was 48.0 ± 26.2 g (n = 5). All nests consisted of two layers, which were weighed separately. The outer layer was composed of dry bamboo (Guadua spp.) and dicotyledonous tree leaves, small roots, twigs, and fresh leaves of fern, and weighed 34.8 ± 25.3 g (n = 5). The proportion of materials used varied among nests with some having almost exclusively dry material (85%) in the outer layer while others had an equal proportion of dry and green materials (50%). The inner layer was mainly small pale brown rootlets (80%), and dry and fresh leaves (20%); it weighed 12.9 ± 3.2 g (n = 5).

The earliest nest was found on 28 August and the latest on 7 December, both with recently laid eggs; no developed embryo was visible when eggs were viewed against a bright flashlight. All nests had a clutch size of two. Egg color was highly variable among nests; four nests contained immaculate white eggs, while seven contained white eggs with brown speckles that ranged from sparsely to heavily speckled (Fig. 1). The eggs weighed an average (± SD) of 3.50 ± 0.33 g (range = 2.85–4.10 g, n = 23); and had an average length of 23.6 mm (range = 21.8–24.9 mm, n = 23) and a width of 17.4 mm (range = 16.1–17.9 mm, n = 23).

Provisioning Behavior and Nestling Growth.—Eggs in only two nests hatched due to predation and abandonment. The first hatched on 25 September and, although the chick was not measured until 28 September, it was possible to delineate hatching day by changes in incubation patterns recorded by the temperature sensors. The chick weighed 8.14 g on day 3 after hatching, had closed eyes, fine black down on the back, and small pin feathers covering the wings. The eyes were open on day 9 and the feathers had started to emerge, revealing an olive-gray color on the
FIG. 1. Eggs of the Pectoral Sparrow (*Arremon taciturnus*) in the foothills of Manu National Park, Cusco, Peru.

Wings and flanks. The nestling gained on average 2.53 g per day between days 3 and 11. It weighed 28.4 g on day 11, the eyes were completely open, and the body and wing feathers opened further revealing olive and yellow coloration. Further measurements were not possible because the nest was empty on day 12, presumably due to predation. No tarsal measurements were taken for this nestling. Two chicks hatched from a second nest on 9 November. Their eyes were closed at hatch, the body was naked except for fine black down on the back, the interior of the mouth was bright red, and the beak was yellow.

The young weighed 3.2 and 2.6 g and had a tarsus length of 5 and 6 mm, respectively. On day 1 they weighed 5.4 and 4.1 g and had tarsus lengths of 6 and 7 mm. They gained mass at a rate of 2.2 and 1.5 g per day, respectively. The nest was empty on day 2; the nest camera revealed an unidentified marsupial depredated the nest during the night.

The male provisioned the nestlings on 16 occasions over a 3-day period at the first nest, the female on five occasions and, in 10 cases, it was not possible to identify the gender of the parent. We recorded three events when the male fed the female while she was brooding the nestlings during day 4 after hatching. The food was too small and mashed for recognition in most cases; however, in three instances it was possible to observe what appeared to be insect parts. The male continued to provide most of the food to the nestlings (76%), even after the female stopped brooding. Removal of fecal sacs was solely by the male. It was not possible to ascertain whether or not the sacs were eaten.

None of the 15 nests was successful. Nine nests were depredated during the egg period, two during the nestling period, and four were abandoned for unknown reasons a few days after we started to monitor them. We made efforts to minimize nest disturbance, but observer interference cannot be ruled out as the reason for abandonment.

**Incubation.**—The longest incubation period recorded was 15 days. The laying date was unknown for this nest, but we believe the eggs were laid 1 or 2 days before being found since no embryo development was observed. Thus, the incubation period is likely between 15 and 17 days. The female was the sole incubator based on our observations, photographs, and videos.

The female had few but long absences each day (Fig. 2). On average the female conducted 74 trips per day (range = 4–10 trips, n = 18 days). Average trip length was 46.4 min (n = 18 days). The longest absence from the nest was 26.3 min, while the shortest was 6 min. On average, the female spent 57% (range = 20–65%, n = 18 days) of daylight incubating the eggs. The on-nest periods ranged from 8 to 323 min with an average of 71.7 min (n = 18 days). The female spent the night incubating in all nests, except for one instance, when the female spent the night outside the nest.

The female spent on average (± SD) 61 ± 3.7% of daylight incubating between days 4 and 10 in the nest that lasted 15 days with no trips longer than 60 min. In contrast, the female spent 55 ± 1.6% of daylight incubating between days 11 and 14 before hatching and 20% of trips were >60 min. Thus, females decreased on-nest time before egg hatching by 6 ± 1.3%, when 12% of the trips lasted >1 hr.
The overall average (± SD) nest temperature was 27.9 ± 1.86 °C (n = 28 days) and average nest temperature was 29.2 ± 2.64 °C (n = 28 days) during incubation periods. Nest temperature decreased to an average of 26.6 ± 2.43 °C (n = 28 days) during incubation recess. Overall average egg temperature was 32.0 °C (range = 20.1-37.6 °C, n = 12 days); and 34.8 °C (range = 27.7-36.0 °C, n = 12 days) when the female was on the nest; egg temperature decreased to 24.0 °C (range = 18.4-36.1 °C, n = 12 days) during foraging trips.

**DISCUSSION**

Ours is the first study comparing behavioral differences within *Arremon*. It is of interest that nest architecture for two of the new species recently added to the genus, *A. brunninuchu* and *A. torquatus* (Cadena et al. 2007) differ greatly from other congeners. These two species nest in open cups in the foliage (Skutch 1954, Skutch and Stiles 1989), while the remaining species with known nests construct closed domes at ground level (Santhluge 1935, Skutch 1954, Havercschmidt 1968, Tye and Tye 1992, Auer et al. 2007).

All nests of Pectoral Sparrow were domed structures, similar to those described for other members of the genus (Skutch 1954, Havercschmidt 1968, Tye and Tye 1992, Auer et al. 2007). They were in predictable places (slopes next to creeks). Egg coloration was variable among females and incubation was solely by the female, which spent on average 61% of the daylight incubating and conducted on average 7.4 trips per day each lasting on average 46.4 min. The male supplied most of the food, although both parents provisioned the nestlings.

**Nest and Eggs.—** Dome nesting species within *Arremon* had similar nest locations and materials; average nest height for *A. flavirostris* and *A. taciturnus* was 0.0 m (range = 0.0-0.9 m, n = 54) and 0.1 m (range = 0.0-1.0 m, n = 15), respectively (Auer et al. 2007). In contrast, cup-nesting species, *A. brunninuchu* and *A. torquatus*, place their nests in vine tangles or bamboo between 1.2 and 8.3 m above ground with two nests recorded >20 m above ground (Skutch 1954, Skutch and Stiles 1989, Auer et al. 2007). Nest material also differed between cup- and dome-nesting species. Both have an external layer composed mostly of dead leaves and an inner lining of rootlets, but none of the cup-nesting species was reported to use green material, while all ground-nesting species have been reported to use green materials (moss, ferns, leaves or grasses) in the outer layer (Skutch 1954, Schulenberg and Gill 1987, Tye and Tye 1992). The use of green materials in nests of *A. aurantirostris* and *A. castaneiceps*, as in *A. taciturnus*, appears to function to blend the nest with the surrounding
Nest characteristics are a part of the extended phenotype that have been useful in reconstruction of avian relationships (Winkler and Sheldon 1993, Zyskowski and Prum 1999). Most of the species in the genus *Arremon* (Snethlage 1935, Skutch 1954, Haverschmidt 1968, Tye and Tye 1992, Auer et al. 2007) build dome nests on the ground. However, based on the latest phylogeny of the group (Cadena et al. 2007, Florez-Rodriguez et al. 2011), two additional species are now included in *Arremon* (A. torquatus and A. brunnneinucha; previously placed in the genus *Bunaremon*). These species are not basal and build cup nests above ground (Skutch 1954, Skutch and Siles 1989), suggesting the cup nest shape derived from the dome nest in the genus *Arremon*.

Egg coloration of *A. taciturnus* varied greatly between nests, ranging from glossy white to glossy white lightly or heavily spotted with brown speckles. Similarly, *A. castaneiceps* eggs were first reported to be white with heavy red spotting at the larger end (Sclater and Salvin 1879), and later described to be immaculate white (Snethlage and Gill 1987). This difference was suspected to be due a mistaken label or species identification by Sclater and Salvin (Schulenberg and Gill 1987). The variability in *A. taciturnus* eggs could account for the differences reported in *A. castaneiceps* eggs, as both colorations were found in *A. taciturnus* eggs. Egg color variation may be common across the genus.

Incubation.—The incubation period of *A. taciturnus* appears to be similar to other *Arremon* members, based on the longest observed incubation period, which incubate between 15 and 17 days (Skutch 1954, Martin 2002). Nest attentiveness in *Arremon* is also remarkably similar among species. *A. taciturnus* had 57% nest attentiveness, *A. flavirostris* 62%, and *A. torquatus* 55% (Auer et al. 2007); all are below the average for neotropical passerines (69%; Martin et al. 2007). Average egg temperature for *A. taciturnus* was 32.0°C at an average ambient temperature of 24.4°C. The average egg temperature for other neotropical passerines species is 34.4°C at an average ambient temperature of 20°C (Martin et al. 2007). Despite being in a warmer climate, *A. taciturnus* eggs had a lower temperature. Ambient temperature could have, and does on many occasions, an effect on egg heat loss but the role the nest has on heat regulation is not well understood (Ar and Sidis 2002). Thus, inter- and intra-specific variation in egg heat loss cannot always be attributed to ambient temperature. Lower temperature of *A. taciturnus* eggs may be caused by long foraging trips by the female (on average 46.4 min, resulting in a 10.8°C difference between average egg temperature during off bouts (24.0°C) and on bouts (34.8°C). Birds may decrease the number of trips to the nest to reduce nest predation risk (Ghalambor and Martin 2002); the high predation risk in our study site may contribute to the low egg temperature and low nest attentiveness observed.

Average body mass of *A. taciturnus* of 26.7 g (Dick et al. 1984). In relation to egg (3.5 g) and clutch mass (7.2 g), was similar to the proportion observed in several neotropical passerine species subject to high predation rates (Martin et al. 2006). This pattern may suggest reproductive investment is reduced by reducing clutch mass rather than egg mass with clutch mass being lower in species with high predation rates (Martin et al. 2006).

Nestling Growth, Provisioning, and Brooding.—The male supplied most of the food to the young once the eggs hatched. Most (76%) of the provisioning visits were by the male and only 24% by the female, based on 21 feeding visits where gender of the parent was known. A similar proportion was reported for *A. aurantiirostris* (male 75% and female 25%; Skutch 1954). The breeding strategies of *A. taciturnus* include small clutch sizes with large eggs, female only incubation, low nest attentiveness, and the male as the main food provider; these are common strategies among neotropical passerine and are shared by all members of *Arremon* (Skutch 1954, Auer et al. 2007). The only aspect with nesting inconsistency among members of the genus is nest shape, placement, and material between the dome- and the cup-nesting species. These nesting differences are insufficient to support splitting of the genus. Analysis of behavioral differences among the traditional genera *Arremon*, *Bunaremon*, and *Lysurus* paired with research on the genetics of the expanded *Arremon* genus may help resolve the phylogenetic relationships of the genus.

ACKNOWLEDGMENTS

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also thank SERNAP for allowing us to work in Manu National Park. Financial support was provided by the Katherine Ordway Foundation, the Dexter Fellowships in Tropical Conservation, Asociacion para la Conservacion de la Cuenca Amazonica (ACCA), and the Wilson Ornithological Society Louis Agassiz Fuertes Award.

LITERATURE CITED


Breeding Success and Nest Site Selection by a Caribbean Population of Wilson’s Plovers

Adam C. Brown1,2 and Kevin Brindock1

ABSTRACT.—We report breeding success of Wilson’s Plovers (Charadrius wilsonia) on St. Martin in the Lesser Antilles during 2004. We located 35 nests among six wetlands and apparent nest success was 31%. Nest initiation on St. Martin was earlier than in the United States and breeding success was higher earlier in the season than later in the season. There were two distinct peaks in nest initiation; the second peak coincided with peak fledging of chicks from the first nest initiation. Nests on St. Martin were associated with bare ground and were much closer together than in previous studies reported elsewhere. Ten nests were predated by feral dogs (Canis lupus familiaris) and three nests were crushed by vehicles. Received 12 December 2004. Accepted 15 April 2011.

Wilson’s Plover (Charadrius wilsonia) is distributed along coastal habitats extending from North America to South America including the West Indies (Corbat and Bergstrom 2000). Populations of the Caribbean race (C. w. cinnamonus) occur in the Bahamas, Greater Antilles, Virgin Islands, and throughout the Lesser Antilles (Hoogerwerf 1977, Collazo et al. 1995, Raffaele et al. 1998, Smith and Smith 1999). The most recent global population estimate of Wilson’s Plover is 6,000 individuals; however, this number is tenuous as the estimate was provided with a low level of confidence (Brown et al. 2001). Wilson’s Plovers are listed as a Species of High Concern in the U.S. Shorebird Conservation Plan due to a low population estimate (Brown et al. 2001). The primary threat to Wilson’s Plovers in the United States is habitat loss resulting from development (Corbat and Bergstrom 2000).

There has been little research on Wilson’s Plovers in the West Indies; thus, there are currently no population estimates for the region and breeding ecology in this area is poorly understood. The absence of population estimates and data on breeding ecology of Wilson’s Plovers in the Caribbean, highlight the need for further study to understand the status of this species in the region and to guide conservation efforts to maintain this population. We studied a breeding population of Wilson’s Plovers on St. Martin, Lesser Antilles in 2004. Our objectives were to: (1) investigate attributes of the plover’s nesting ecology and, (2) factors affecting breeding success.

METHODS

Study Area.—St. Martin, Lesser Antilles (18° 03’ N. 63° 03’ W; 100 km²) includes several breeding sites used by Wilson’s Plovers, making it a suitable study area to examine their breeding ecology. The island includes 21 wetland sites providing suitable nesting habitat for this plover. Sites ranged in size from 0.136 to 2.2626 ha. Every wetland was surrounded by vegetation comprised mainly of red mangroves (Rhizophora mangle), black mangroves (Avicennia germinans), white mangroves (Laguncularia racemosa), buttonwood (Conocarpus erectus), and sea-grape (Coccoloba uvifera). There was sparse mangrove vegetation scattered throughout the wetlands as well. Each wetland was surveyed from multiple observation points, assuring the shoreline of each wetland was observed in its entirety.

Nest Observations.—We surveyed all sites (n = 21) on St. Martin from 1 January through 30 July 2004, every 5 days using binoculars and spotting scopes to detect breeding shorebirds (Fig. 1). Once a Wilson’s Plover was detected, observers recorded the bird’s behavior, including that suggestive of active nesting, such as birds flying back-and-forth towards a specific spot, males chasing other birds in the hunched-over territorial, mock-brooding, or broken-wing displays (Bergstrom 1988). We then approached the area where the bird was observed and searched all adjacent suitable habitats in a grid-like pattern for a nest scrape. Plover tracks were often followed to help observers locate the nest scrape. Observers estimated and recorded the stage of nesting.
short communications 815

(occupied scrape, number of eggs, and number of chicks) and date once a nest was located. We recorded the contents of the scrape from the center out for 10 cm documenting presence or absence of shells, vegetation, rocks, and bare ground in the immediate area of the nest scrape.

Visits were conducted every 5 days to record the current nest contents following the initial detection of a nest scrape. Nests were considered successful when ≥1 chick hatched, and unsuccessful (failed) when no chicks were produced from the nest. We surveyed the area for signs suggesting cause (i.e., tracks from a predator leading to the nest) in the event a nest failed. We recorded number of chicks and their feathering status during each survey once chicks hatched and were mobile. Chicks were not marked but nest origins were generally identifiable by their geographic location and large space between active nests with chicks. Chicks were followed until the end of the survey period, but were considered fledged after 21 days (Tomkins 1944).

We attempted to identify the cause of disappearance of chicks before fledging.

We returned to the nest to collect data characterizing the habitat near the nest once a nest scrape was abandoned following hatching or nest failure. A 2-m radius from the center of the scrape was surveyed within which we recorded the percentage of live vegetation, dead/woody vegetation, rock, and bare ground using 5% increments.

RESULTS

We found 35 Wilson’s Plover nests on St. Martin: 15 at Orient Pond, 10 at Grand Etang, five at Gallion Pond, three at Etang Poisson, and one each at Grand Case Pond and Simpson Bay Lagoon (Fig. 1). Nineteen chicks fledged from the 35 nests (Table 1). The mean (± SD) clutch size was 2.37 ± 0.597 and the mean laying date was 13 April (range = 28 Feb–7 Jun). There were two one-egg clutches, 18 two-egg clutches, and 15 three-egg clutches. The mean number of chicks/
TABLE 1. Number of nests initiated and apparent nest success at Wilson's Plover nest sites during 2004 on St. Martin.

<table>
<thead>
<tr>
<th>Weekend</th>
<th>Total attempts</th>
<th>Apparent successful nests</th>
<th>First nest initiated</th>
<th>Mean eggs/pair</th>
<th>Mean chicks/pair</th>
<th>Mean fledge/pair</th>
<th>Area of colony (ha)</th>
<th>Mean distance between nests (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orient</td>
<td>45</td>
<td>3</td>
<td>3 Mar</td>
<td>2.20 ± 0.59</td>
<td>0.26 ± 0.59</td>
<td>0.20 ± 0.41</td>
<td>1.5374</td>
<td>139</td>
</tr>
<tr>
<td>Grand Etang</td>
<td>10</td>
<td>6</td>
<td>21 Mar</td>
<td>2.70 ± 0.48</td>
<td>1.00 ± 1.05</td>
<td>0.90 ± 0.99</td>
<td>0.1360</td>
<td>14.5</td>
</tr>
<tr>
<td>Gallion</td>
<td>9</td>
<td>1</td>
<td>3 Mar</td>
<td>2.20 ± 0.45</td>
<td>0.40 ± 0.89</td>
<td>0.40 ± 0.89</td>
<td>0.1353</td>
<td>15.4</td>
</tr>
<tr>
<td>Etang Pousson</td>
<td>3</td>
<td>2</td>
<td>10 Mar</td>
<td>2.66 ± 0.57</td>
<td>1.00 ± 1.00</td>
<td>1.00 ± 1.00</td>
<td>0.2399</td>
<td>17.3</td>
</tr>
<tr>
<td>Grand Case</td>
<td>1</td>
<td>1</td>
<td>28 Mar</td>
<td>2.00</td>
<td>2.00</td>
<td>2.00</td>
<td>0.4943</td>
<td>N/A</td>
</tr>
<tr>
<td>Simpson Bay Lagoon</td>
<td>1</td>
<td>0</td>
<td>10 May</td>
<td>2.00</td>
<td>0.00</td>
<td>0.00</td>
<td>2.2626</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Apparent nest success was 0.6 ± 0.768 with 25.3% of total eggs hatching; mean hatching date was 16 April (range = 28 Mar–26 Apr). The mean (± SD) number of fledged chicks/nest was 0.54 ± 0.707 with 90.5% of chicks fledging; the mean fledging date was 7 May (range = 18 Apr–17 May) (Fig. 2).

Apparent nest success, the proportion of observed nesting attempts that succeeded, was 37.1%, but varied among sites. Orient Pond, the site with the most nesting attempts (n = 15) and most failed nests, had 20% apparent nest success. The next largest population, Grand Etang (n = 10) had 60% apparent nest success. Gallion Pond, the third largest colony (n = 5), had 20% apparent nesting success. The smaller populations had more widespread nest success, Etang Pousson (n = 3) had apparent nest success of 67%. Grand Case (n = 1) had an apparent nest success of 100%. and Simpson Bay Lagoon (n = 1) had an apparent nest success of 0%.

There were two peaks in nest initiation: 3–21 March and 10–26 May (Fig. 2). Nests that successfully fledged at least one chick were...
TABLE 2. Wilson's Plover nest-habitat and nest-scrape descriptions. Values reported in habitat adjacent to the nest are the mean percentages for each site. Values reported in nest-scrape content are the percentage of nests per location that contained the content. Percentages were estimated to the nearest 5%.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Habitat adjacent to nest</th>
<th>Nest scrape contents</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Percent live vegetation</td>
<td>Percent dead</td>
</tr>
<tr>
<td>Orient</td>
<td>35</td>
<td>2</td>
</tr>
<tr>
<td>Grand Etang</td>
<td>44</td>
<td>11</td>
</tr>
<tr>
<td>Gallion</td>
<td>27</td>
<td>6</td>
</tr>
<tr>
<td>Etang Poisson</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>Grand Case</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>Simpson Bay Lagoon</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

generally initiated earlier than those that were unsuccessful (successful: n = 13, mean date = 17 Mar; unsuccessful: n = 22, mean date = 29 Apr). Apparent nest success was higher in the earlier part of the nesting season when 75% of nests initiated prior to the mean laying date (28 Feb–13 Apr; n = 16 attempts) were successful. Nests initiated after the mean laying date (14 Apr–23 Jun; n = 19 attempts) had an apparent nest success of 5%.

We documented the probable cause of failure for 13 of the 22 nests that failed through identification of tracks leading to and away from the nest scrape. Ten nests were predated by feral dogs (*Canis lupus familiaris*) and three nests were crushed by vehicles. We could not identify the cause of failure for nine nests. Seven of the nine nests were predicted to hatch near the period of our nest check, and failure could have been with either the eggs or the chicks. The eggs in two of the failed nests disappeared well before the predicted hatching date, suggesting egg predation.

Wilson's Plover nests were on the shorelines of saltwater ponds surrounded by mangroves. All wetlands with plover colonies were within 250 m of small towns or housing establishments (mean distance = 106.09 ± 0.248 m). All nests were on flat ground within 0.25 m of pond elevation level. The sediment at all nest locations was fine-sized light-colored sand. Nest scrapes included a mix of shells, vegetation, rocks, and bare ground (Table 2). We observed shells in 48.6% of nests, vegetation in 51.4% of nests, rock in 51.4% of nests, and bare ground in 100% of nest scrapes. The mean distance between nests within colonies with multiple nests, was 14.7 m (n = 23; range = 10–19 m).

We used the percentage at each nest of the four habitat parameters (live vegetation, dead vegetation/woody debris, rock, and bare ground) recorded within a 2-m radius of the nest center to calculate mean nest habitat. The mean nest habitat was 52% bare ground, 34% live vegetation, 9% rock, and 5% dead vegetation/woody debris (Table 2). Five nests were surrounded by 100% bare ground, including three that successfully fledged chicks.

DISCUSSION

Apparent nest success of Wilson's Plovers on St. Martin was similar to that reported in the United States. Causes for nest failure on St. Martin were comparable to those reported at other breeding sites, mainly mammalian predation and human disturbance.

Introduced predators were a common threat to breeding Wilson's Plovers on St. Martin. Dogs were often observed near one of the breeding sites beginning in late May, near the time of a potential peak in chick hatching. Dogs were not observed eating eggs or chicks, but dog tracks were identified approaching and leaving nest scrapes during nest checks when eggs were initially observed missing. Predation by rats (black [*Rattus rattus*] and Norway [*R. norvegicus*]) and Indian mongoose (*Herpestes javanicus*), which are present and common on St. Martin (Brown 2008), may explain failure of nine additional plover nests where shell fragments were found near nests.

Human disturbance was also identified as a cause of nest failure on St. Martin. All locations where Wilson's Plovers bred on St. Martin were within 250 m of housing developments. Vehicles were often observed driving to and from developments across wetlands and subsequently drove over and crushed eggs in three different plover nests. Repeated disturbance by vehicles traveling through the nesting colony may have caused adult
plovers to abandon nesting attempts, explaining failure of nine nests where cause of failure was not identified.

Nesting Wilson’s Plover began earlier on St. Martin than described for populations within the United States. Wilson’s Plover nests in the United States with the exception of a single March nest initiation date are initiated in April (Stevenson and Anderson 1994, Corbat and Bergstrom 2000). Bergstrom (1988) reported the first nest initiation on 15 April in Texas with two distinct peaks, 21–29 April and 18–31 May. Corbat (1990) reported the first nests occurred in Georgia in mid-April and nesting continued through June. Nest initiation on St. Martin appeared to occur at wetlands once ponds were nearly dry and provided adequate area for nesting attempts. There was little open shoreline along ponds prior to drying, likely inhibiting nesting due to lack of suitable habitat.

The second nest initiation peak in mid-May coincided with fledging of young for pairs that nested during the first nest initiation peak. Multiple peaks have been described in previous breeding descriptions (Bergstrom 1988), that have been attributed to re-laying efforts of birds whose attempts during the first nest initiation period failed. This was likely the case on St. Martin. There is a single record of a Wilson’s Plover re-laying after a successful nesting attempt in the United States (Corbat 1990) and, with the extended breeding season on St. Martin, this may be a possible explanation as well.

Pairs that initiated nests earliest had the highest breeding success. It is possible dogs, which may have depredated 10 of the later initiated nests, did not detect the plover colony until later in the season when nest density increased. Small amounts of water in the ponds early in the breeding season would have limited vehicle access to these areas, decreasing the likelihood that an earlier nest would be destroyed by a vehicle.

Spacing between nests at sites on St. Martin was different than at sites in the United States. Spacing between nests in wetlands was close (mean distance = 14.7 m). Bergstrom (1988) reported greater distances between nests in Texas with the closest nests 35.5 m and most nests were >250 m distant. The closeness of nesting plovers on St. Martin is likely due to the limited amount of suitable nesting habitat on the island.

The amount of vegetation and other objects near nest scrapes appears similar to populations described in Texas (Bergstrom 1988) and Georgia (Corbat 1990). All nests were in areas that were underwater during the wet season and early part of the dry season (Sep–Feb); little vegetation grew in these areas due to the hyper-saline nature of the ponds (90 ppt). Nest scrapes were most often in areas containing primarily bare ground with limited cover (vegetation or debris). The presence of cover or objects near nests may limit the ability of plovers to detect predators, decreasing nest success.

Mammalian predation and human disturbance issues on St. Martin are due in large part to increased development of coastal and wetland areas. The available wetland habitat for plovers to breed and forage is decreasing as development on the island increases. St. Martin has recently taken steps in protecting wetland habitat, but enforcement to protect wetlands from encroachment by development is lacking and remains important in protecting critical plover habitat.

ACKNOWLEDGMENTS

We thank the Reserve Naturelle on St. Martin for allowing access to the wetlands of the Reserve on the French side of St. Martin. We thank Natalia Collier for assistance in the field and for reviewing an earlier draft of the manuscript. We appreciate the suggestions of Sean McAllister and the reviews by J. A. Jackson, C. E. Braun, and an anonymous reviewer that improved the manuscript. This is EPIC Publication Number 50.

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Description of the Nest and Egg of an Atlantic Forest Endemic, the Black-headed Berryeater, *Carpornis melanocephala* (Cotingidae)

Ricardo Belmonte-Lopes, Giovanni N. Maurício, and Marcos R. Bornschein

**ABSTRACT.**—We describe the nest and egg of the Black-headed Berryeater (*Carpornis melanocephala*), an Atlantic Forest endemic considered vulnerable to extinction. The nest was in a montane evergreen primary forest area in a tree fork 4.2 m above the ground. It was cup shaped and constructed mainly of leaves and stems, resembling a pile of aerial leaf litter. It held just one egg that was incubated solely by the female. The male was near the nest, and inspected it once while being observed. 

**METHODS**

We describe a nest and egg of the Black-headed Berryeater from the Serra das Lontras (15° 09' 46" south, 54° 17' 53" west).
FIG. 1. Nest of the Black-headed Berryeater (Carpornis melanocephala) viewed from below. The arrow indicates the nest. Photograph by RB-L.

S, 39° 20′ 25″ W, 785 m asl) on the property of the Instituto de Estudos Socioambientais do Sul da Bahia (IESB), Arataca municipality, Bahia State, Brazil. A pair of Black-headed Berryeaters was observed constantly active in a limited area between 1 and 2 September 2006. We identified the two birds as a male and a female, paired, and assumed they might have had an active nest nearby. We followed them as closely as possible, choosing as main targets the points at which the male perched to sing. We observed the male singing at several points, and a nest-like structure was finally detected ~2 m from one of these points. We focused attention at that structure which proved to be an active nest of *C. melanocephala*. Two observers performed ~2 hrs of focal observations of the nest from concealment >15 m from it.

The nest and egg were collected for deposition in the ornithological collection of the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP). Nest height above the ground was measured with a 5-m tape measure, from the upper border of the nest to the ground. Measurements of the nest and egg were taken with calipers to the nearest 0.1 mm. Capitalized color names and respective numbers in the egg description follow Smith (1975).

**RESULTS**

On 2 September 2006, after ~3 hrs of observations, we saw the female flying and perching in a structure that initially resembled a pile of aerial leaf litter (Fig. 1). We realized the structure was actually a nest only after the female remained perched at the site. A pair of Black-headed Berryeaters was constantly present during our observations of the nest site. Only the female incubated the sole egg, while the male remained in the immediate vicinity and once perched on the nest, apparently inspecting the egg.

The nest was inside a 20–25 m tall primary evergreen forest. It was on a 6-m tall tree with a diameter at breast height of 0.1 m. The tree was isolated from direct contact with other trees, partially because of wood coppicing. The nest was 4.2 m above the ground in a fork 0.35 m from the main tree trunk. It was supported laterally by the two fork stems (diam = 10.8 and 12.8 mm) and also by a smaller stem (8.9 mm in diam) that projected from one of the main stems and formed a smaller, second fork. The nest was primarily supported by a bromeliad leaf, 43.4 mm in width, curved at an angle of 70° below the two forks, providing support for most of the nest structure. The nest had an external diameter of 117.9 × 99.5 mm and an external height of 109.7 mm. The
incubation chamber had a diameter of 62.8 × 87.9 mm and was 41.1 mm deep.

The nest was mainly composed of dry leaves (whole leaves and fragments); most of the leaves were presumed to be from the same tree species in which the nest was attached. The outer walls of the nest were supported by dry stems with diameters between 5.0 and 5.8 mm, and other bromeliad leaves. The nest was lined with dry leaves and several thin stems (diam ≤0.9 mm).

The nest had only one egg measuring 33.2 × 23.5 mm (Fig. 2). The egg’s background color was Pale Horn (92) with small spots and stripes of Verona Brown (223B); the larger end was uniformly colored Grayish Horn (91).

DISCUSSION

Our observations of the female and male attending the nest suggest the Black-headed Berryeater has biparental care of nestlings, as also reported for the cotingid genera Pipreola (Pipreolinae), Phytotoma, and Zatarornis (Phytotominae), and Coniptilon (Cotinginae) (Snow 1982, 2004b; Celis et al. 2006; Rosina and Romo 2010). These genera (with exception of Coniptilon) are basal in the Cotingidae phylogeny (Tello et al. 2009) and it is possible that biparental care represents an ancestral characteristic in the family.

Inconspicuousness is an obvious way to avoid nest predation and, since many Cotingidae nests are very small, it is hypothesized these structures evolved under predation pressures (Snow 1982). The nest of the Black-headed Berryeater is another example of adaptation to these pressures. It is inconspicuous, not because of its size but, due to its external appearance, which reassembles a pile of aerial leaf litter.

The nest could be described as 'cup shaped' attached as 'top lip' (following Hansell 2000), or as 'low cup' attached as 'fork' (following Simon and Pacheco 2005). The nest of the Black-headed Berryeater was constructed using the 'piling up' and 'interlocking' techniques (following Hansell 2000). The technique of 'interlocking' is divided into four different methods of construction (Hansell 2000) from which the Black-headed Berryeater used 'entangle' (in which the bird shapes the materials to bind together) and 'velcro' methods (which uses animal silk to fix the nest to vegetation). The use of the 'entangle' is known in the Cotingidae (Snow 1982), but the use of 'velcro' has not been reported before in the family, requiring confirmation by direct observations.

Collar et al. (1992) reported specimens of the Black-headed Berryeater with gonads half or little enlarged in June \( n = 1 \), female, November \( n = 1 \), male, and December \( n = 2 \), males) and others with no enlarged gonads in June and December (2
males and 1 female, respectively) at Espírito Santo State and southern Bahia. Collar et al. (1992) considered the evidence of breeding from the size of the gonads is consistent with greater vocal activity in December in Espírito Santo State. Thus, given this evidence and the nest record reported here, we assume the species' reproductive season probably occurs between August and January.

The laying of only one egg is common in almost all medium-sized and large Cotingidae (Snow 2004b). However, it is known to be a typical feature of polygynous species but not monogamous taxa such as Carpinis (Snow 1982). We assume the sole egg was the complete clutch, since after examination, we found a large embryo occupying between one third and half of the egg’s internal volume. Kirwan (2009) observed two fledged young of Hooded Berryeater accompanying and soliciting food from at least one adult, suggesting a clutch size of two eggs. However, exhaustive observations of Hooded Berryeaters from the incubation period to the fledgling stage reveal that it lays only one egg per clutch, although a given breeding pair may rear up to 2-3 young during the entire breeding season (GNM, unpubl. data). The egg of the Black¬

headed Berryeater described here is similar in shape, size, and color to those of the Hooded Berryeater (von Ihering 1900; GNM, unpubl. data), being within the range previously described for the Cotingidae (Snow 2004b).

ACKNOWLEDGMENTS

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LITERATURE CITED


Responses of Nesting Yellow-headed Blackbirds and Yellow Warblers to Wrens

Diane L. H. Neudorf,1,2 Katherine E. Sears,1 and Spencer G. Sealy2

ABSTRACT.—We studied nest defense behavior of Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) and Yellow Warblers (Dendroica petechia) in response to two species of common nest destroyers. We presented freeze-dried models of Marsh Wrens (Cistothorus palustris) at Yellow-headed Blackbird nests and House Wrens (Troglodytes aedon) at Yellow Warbler nests during the incubation stage. We presented a Clay-colored Sparrow (Spizella pallida) as a control for both species. Male Yellow-headed Blackbirds responded more intensely to the Marsh Wren model than the control, and female blackbirds responded intensely to both models but were more aggressive toward the Marsh Wren. Most Yellow Warblers did not respond to the House Wren model with their typical predator responses (e.g., chip alarm calls). Some female warblers were aggressive toward the wren model, whereas others sat in their nest. Sitting in the nest as a defense to deter nest destruction by House Wrens needs further investigation. Differences in response levels between blackbirds and warblers may be related to differences in levels of nest destruction experienced by the two species or differences in nest defense behaviors used by the two species. Received 15 September 2010. Accepted 28 March 2011.

Several experiments have demonstrated that Marsh (Cistothorus palustris) and House (Troglodytes aedon) wrens peck and attempt to destroy eggs regardless of their size (Picman 1977, White and Kennedy 1997). Eggs and nesting material may be removed from destroyed nests (Belles-Isles and Picman 1986) and both species, at times, kill or injure nestlings (Belles-Isles and Picman 1986, Picman and Isabelle 1995). Eggs of conspecifics and heterospecifics are often destroyed but typically are not eaten. Explanations for nest destruction behavior include reduced competition for food (Picman 1977), as well as reduction of reproductive success of competitors (Belles-Isles and Picman 1986). House Wrens are secondary-cavity nesters and may destroy nests to gain nest sites (Quinn and Holroyd 1989, Pribil and Picman 1991), although they also destroy eggs and nestlings in open-cup nests (Belles-Isles and Picman 1986).

Species nesting in the vicinity of wrens, given the potential threat of nest destruction, should respond aggressively to them. Nest defense is a common behavior of birds to protect their nests and offspring from predators (Montgomerie and Weatherhead 1988) and avian brood parasites (Sealy et al. 1998). Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) experience considerable nest destruction from Marsh Wrens. Picman and Isabelle (1995) used cameras and egg damage to demonstrate that —11% of natural nests and 40% of artificial nests were destroyed by Marsh Wrens during their study in Manitoba. Yellow-headed Blackbirds respond aggressively toward playbacks of wrens near their nests (Bump 1986, Picman and Isabelle 1995). Nesting Yellow Warblers (Dendroica petechia) and House Wrens co-occur in upland forest areas in southern Manitoba. We have not observed Yellow Warblers behaving aggressively toward wrens and have not recorded egg damage caused by wrens in our study area (S. G. Sealy, pers. obs.). However, we were interested in examining if Yellow Warblers respond given that House Wrens are common in our study area and their potential for nest destruction (White and Kennedy 1997).

Previous studies of Yellow-headed Blackbirds (Sealy et al. 1998) and Yellow Warblers (Hobson et al. 1988, Gill and Sealy 1996) demonstrated these species defend their nests against egg and nestling predators, and also against brood-parasitic Brown-headed Cowbirds (Molothrus ater). We tested recognition abilities of Yellow-headed Blackbirds by presenting freeze-dried models of Marsh Wrens at their nests to examine their response to a visual stimulus of this nest destroyer. We predicted Yellow-headed Blackbirds should respond more intensely to the Marsh Wren mount than an innocuous control. We
recorded responses of Yellow Warblers to freeze-dried House Wren models placed at their nests to examine if they respond more intensely to the wren model than an innocuous control.

**METHODS**

**Study Site.**—We tested active nests of Yellow Warblers in June 1991 and nests of Yellowheaded Blackbirds from late May to early June 1992 on and around the Delta Marsh Field Station (University of Manitoba), along the south edge of Lake Manitoba. Yellow Warblers nested in the forested dune ridge that separates Lake Manitoba from Delta Marsh; Yellow-headed Blackbirds nested in Delta Marsh. House and Marsh wrens nest commonly in the study area.

**Models.**—We presented active nests of Yellowheaded Blackbirds with freeze-dried Marsh Wrens and active nests of Yellow Warblers with freeze-dried House Wrens (hereafter, models). We used a freeze-dried Clay-colored Sparrow (*Spizella pallida*) model as a control in both experiments. We chose the Clay-colored Sparrow as the control because it is similar in size to the wrens but the sparrow does not threaten the nests of either species tested. Clay-colored Sparrows do not nest in the forest or marsh but should be familiar to both blackbirds and warblers because they nest in upland habitats adjacent to nest sites of these species (Hill and Sealy 1994). We used 2–3 models of each species to reduce the effects of pseudoreplication and to replace damaged models.

**Field Procedures.**—We performed the tests in the mid-morning or afternoon during the incubation stage of each species. We chose to test our predictions at the incubation stage when females would be more attentive to the nest and more likely to detect the model. We clipped models to nearby vegetation so they were level with the nests and faced them from a distance of 0.5 m while the nest owners were absent. We recorded our observations at a distance of at least 15 m either from a vehicle (Yellowheaded Blackbird) or hidden behind vegetation (Yellow Warbler). Yellow-headed Blackbirds nesting within the vicinity of roads are habituated to cars parked or passing by and did not react to us when we parked near their nests. Yellow Warblers are fairly tolerant of human observers in our study area and we did not appear to elicit nest defensive responses from them when we hid behind vegetation. We preferred this method of observation to the limited visibility of a blind where birds perched at a distance may be missed. Timing began when the first nest owner returned to the vicinity of the nest. Each nest was tested with both models, sequentially. We assigned order of model presentation randomly for the first nest and then in alternating order to ensure the same number of nests would receive the same treatment. We used a 15-min nest–model period between model presentations. We assumed this time period would be adequate to reduce effects of carry-over aggression as it has been used in previous studies of nest defense in our study area (Briske and Sealy 1989).

Defensive responses included: (1) approach within 2 m of the model, (2) close passes or contact with the model, (3) alarm calls, (4) perch changes (Yellow Warblers only), and (5) time in the nest. Distance, alarm calls, and time in the nest behaviors were measured as the number of 10-sec intervals in which nest owners engaged in that behavior. Close passes or contacts and perch changes were measured as the actual number of times they occurred in the trial. Female Yellowheaded Blackbirds give the squawk alarm call (Sealy et al. 1998), whereas Yellow Warblers use chip calls toward nest predators (Hobson and Sealy 1989, Gill and Sealy 2003).

We initially presented each model for 5 min to Yellowheaded Blackbirds (*n = 7*) and Yellow Warblers (*n = 5*). However, we reduced the trial to 2 min in three of the presentations to minimize damage to the models by aggressive individual Yellowheaded Blackbirds. The most intense defense behaviors (e.g., close passes and contact) for Yellowheaded Blackbirds and Yellow Warblers occurred only in the first 2 min of the trials—75 and 100% of the time, respectively. Our analyses are based on the first 2 min of model presentations for all nests tested for both species. We used nonparametric statistics because our data were not normally distributed. All tests were two-tailed because we were also interested in results that may be counter to our predictions (Lombard and Hurlbert 2009).

**RESULTS**

Yellowheaded Blackbird.—Female Yellowheaded Blackbirds reacted to the models more frequently than males but did not respond significantly differently to the wren compared with the sparrow (Table 1). Females spent similar amounts of time close to both models and alarm called in response to both models. The most
TABLE 1. Responses (mean ± SE) of Yellow-headed Blackbird nest owners to Clay-colored Sparrow (control) and Marsh Wren models presented at 10 nests.

<table>
<thead>
<tr>
<th>Model</th>
<th>Response</th>
<th>Nest owner</th>
<th>Sparrow</th>
<th>Wren</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;2 m</td>
<td>Female</td>
<td>10.3 ± 0.9</td>
<td>9.8 ± 1.2</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Close passes/contacts</td>
<td>Female</td>
<td>4.0 ± 2.1</td>
<td>8.4 ± 4.4</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>Squawk</td>
<td>Female</td>
<td>4.5 ± 1.5</td>
<td>4.7 ± 1.7</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>In nest</td>
<td>Female</td>
<td>4.0 ± 1.4</td>
<td>3.2 ± 1.3</td>
<td>0.38</td>
</tr>
</tbody>
</table>

Categories of distance, squawk calls, and sitting in nest were quantified in 10-sec intervals in which nest owners engaged in that behavior for a maximum of 12 intervals. Close passes/contacts were measured by the number of times the behavior occurred within the trial.

To two-tailed Wilcoxon signed-rank tests.

significant damage by females was to the wren model, and involved sitting on the model's back, pulling apart the model and, in one case, pulling off the model's head. Males tended to spend more time within 2 m of the wren model with more close passes and contacts directed at the wren than the control model (Table 1).

Females and males differed in amount of time within 2 m of the wren model (Wilcoxon signed-rank test, P = 0.05) and sparrow model (P = 0.03) with females spending more time within 2 m of both models. Females gave more close passes/contacts than males to both models, but the number did not differ significantly between males and females toward the wren (P = 0.22) or the sparrow (P = 0.13; Table 1), probably due to small sample sizes.

Yellow Warbler.—Females responded during most trials, whereas males rarely responded (25% of trials), and their responses were not quantified. Males that did respond did not give alarm calls, pass close to or contact the model, or sit in the nest in response to the model. The primary responses of females towards both sparrow and wren models were presence within 2 m and perch changes, although these behaviors did not differ between models (Table 2). High-intensity nest defense responses such as close passes and contacts were rarely given and only in response to the wren. Two female Yellow Warblers responded with close passes and another contacted the wren model (Table 2). Chips were given occasionally but not at high rates and did not differ between models. Females spent more time in the nest in response to the wren and this difference approached significance (Table 2).

DISCUSSION

Yellow-headed Blackbirds apparently recognized the Marsh Wren as a threat to their nest and males in particular responded more aggressively to the wren model than to the control. Our results agree with those of Bump (1986), who found that blackbirds responded aggressively to vocalizations of Marsh Wrens. Previous experiments showed that Yellow-headed Blackbirds chase

TABLE 2. Responses (mean ± SE) of female Yellow Warblers to Clay-colored Sparrow (control) and House Wren models presented at 12 nests.

<table>
<thead>
<tr>
<th>Model</th>
<th>Response*</th>
<th>Sparrow</th>
<th>Wren</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;2 m</td>
<td>9.5 ± 1.0</td>
<td>10.5 ± 0.8</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Close passes/contact</td>
<td>0.0</td>
<td>0.7 ± 0.4</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>Chip</td>
<td>2.8 ± 1.7</td>
<td>1.1 ± 0.5</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>In nest</td>
<td>1.1 ± 0.6</td>
<td>2.5 ± 1.1</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Perch change</td>
<td>8.4 ± 2.0</td>
<td>10.8 ± 2.7</td>
<td>0.87</td>
</tr>
</tbody>
</table>

a Categories of distance, chip calls, and sitting in nest were quantified in 10-sec intervals in which nest owners engaged in that behavior for a maximum of 12 intervals. Close passes/contacts and perch changes were measured by the number of times the behavior occurred within the trial.

b Two-tailed Wilcoxon signed-rank tests.

too many zero differences to perform paired-test.
Marsh Wrens and competitively exclude them from their territories (Leonard and Picman 1986). Female Yellow-headed Blackbirds responded at similar levels of intensity to the wren and the control. Two of 10 blackbird females tested damaged the wren, pulling it apart. The same females were less aggressive toward the sparrow. These findings demonstrate individual variation in responses, which is common in studies of nest defense (Grim 2005, Campobello and Sealy 2010). Past experience with wrens or the age of the female may have a role in recognition and response. Larger sample sizes may have strengthened our case for specific recognition of wrens as threats by blackbirds. Male blackbirds appeared to discriminate between wrens and the control, responding more intensively to the former (Table 1). Females were more attentive to the nest than males and had more close passes and contact to both models. Female blackbirds may respond aggressively to any small species near their nests. Marsh Wrens frequently destroy Yellow-headed Blackbird nests (Picman and Isabelle 1995) and any small species encountered near the nest may be regarded as a potential threat.

Yellow Warblers responded similarly to House Wrens and the control in time close to the model, alarm calls, and perch changes. Yellow Warblers consistently give chip calls in response to egg and nestling predators, and seeet calls toward cowbirds (Gill and Sealy 1996), but they gave few alarm calls when presented with wrens in the present study. However, female Yellow Warblers spent more time in the nest when the wren model was present nearby. This could represent a form of nest-protection behavior as described by Hobson and Sealy (1989). Researchers in previous studies showed that Yellow Warblers rush to sit in the nest and give seeet alarm calls when presented with cowbird models (e.g., Hobson and Sealy 1989, Gill and Sealy 1996). Five of 12 Yellow Warblers in our study sat in their nests in response to the House Wren model and in only one case did the female chip immediately prior to entering the nest.

The differences between warblers and blackbirds in level of response toward wrens may be related to the frequency of nest destruction they experience or differences in nest defense strategies between the two species. Yellow-headed Blackbirds experience frequent nest destruction by Marsh Wrens at our study site (Leonard and Picman 1986, Picman and Isabelle 1995) and they respond aggressively to wren models. We observed the most intense levels of nest defense (close passes/contacts) by blackbirds in seven of the 10 Marsh Wren presentations. We do not know the incidence of egg destruction experienced by Yellow Warblers from House Wrens in our study area. Most Yellow Warblers did not respond to House Wrens with their typical predator response (e.g., chip alarm calls). Some females, however, responded aggressively to the wren model, whereas others sat in their nest. The incidence of nest destruction by wrens and use of nest protection behavior as a deterrent to nest destruction by Yellow Warblers requires further investigation.

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Artificial Nest Cavity Used Successfully by Native Species and Avoided by European Starlings

Laura A. Tyson,1,2 Bradley F. Blackwell,1 and Thomas W. Seamans1

ABSTRACT.—We describe a weather-durable cavity design used successfully by cavity-nesting species native to the eastern USA and, although accessible, avoided by European Starlings (Sturnus vulgaris). The artificial nest cavity was constructed using 9.5-cm inside diameter polyvinyl chloride tubes cut to 27.5-cm lengths. The tubes were mounted horizontally with 5.1-cm entry holes drilled through one of the capped ends. Eastern Bluebirds (Sialia sialis), House Wrens (Troglodytes aedon), and Tree Swallows (Tachycineta bicolor) nested in 49 of 100 newly mounted tubes on utility poles in north-central Ohio, USA from April through June 2009. These species nested in 85% of the tubes during the same period in 2010 and fledged young from 94.1% of nests. We added 10 nest tubes (27.5-cm long x 17-cm inside diam) at sites similar to the smaller tubes in 2010. Two of the larger tubes were used by testing starlings and six by native species. Cavity depth has been shown to be an important feature in starling nest site selection, but our data from the larger tubes indicate that other factors are likely important. The smaller design could offer nesting opportunities for a range of native cavity-nesting species while limiting use by starlings.

Providing artificial nest cavities to increase abundance of secondary cavity-nesting species is viewed as an effective tool (Hamerslrom et al. 1973, Newton 1994, Smith et al. 2005, Catry et al. 2009), although questions remain as to effects on avian community structure (Van Balen et al. 1982, Purcell et al. 1997, Miller 2002, Münd et al. 2005). A variety of studies (Kalmbach and Gabrielson 1921, Brush 1983, Kerpez and Smith 1990, Cabe 1993) have concluded nest competition exists between native cavity-nesting species and European Starlings (Sturnus vulgaris; hereafter starling), but the resulting effects on populations are unclear (Koenig 2003).

Use of artificial nest cavities by secondary cavity-nesting birds can have conservation implications, and placement of nest structures is both popular and educational from the public perspective (Cornell Laboratory of Ornithology, Ithaca, NY, USA: http://www.allaboutbirds.org/NetCommunity/Page.aspx?pid=1139). Thus, artificial cavity designs should consider not only requirements of the target species (Gehlbuch 1994), but also should minimize competitive interactions between native and invasive cavity nesters.

Our original experiment was designed to investigate a potential starling cavity repellent. We discovered avoidance by starlings of our artificial cavities prior to implementing treatments...
and changed our focus to report on successful use of a novel cavity design by native species across cavity size. Thus, we report only descriptive statistics with regard to species and nesting data.

METHODS

We conducted our study on the 2,200-ha National Aeronautic and Space Administration (NASA) Plum Brook Station (PB), Erie County, Ohio, USA. Habitat within PB differs from the surrounding mix of agricultural and suburban area, and is composed of dogwood (Cornus spp.: ~39%), old field and grasslands (~31%), open woodlands (~15%), and mixed hardwood forests (~11%) interspersed with abandoned and actively used structures, and paved roads that circle and restrict Plum Brook Station has restricted public access.

We attached 100, 27.5-cm long × 9.5-cm diameter polyvinyl chloride (PVC) tubes horizontally to utility poles (using pipe straps) (Fig. 1) prior to the 2009 breeding season, maintaining 240 m between each tube. Utility poles on PB are in grass margins (20 to 30 m wide) along roadways and bordering wooded areas. We positioned the tubes facing the roadway to facilitate observations during the experiment, as opposed to maintaining an easterly or southeasterly frontage. Previous experiments with nest boxes on PB reported no effects of entrance direction on starling nesting (Dolbeer et al. 1988, Belant et al. 1998, Seamans et al. 2001, White and Blackwell 2003).

Each tube was placed 3 m above the ground with an aluminum predator guard mounted below the tube. The ends of each tube were sealed with a PVC cap, and the 5.1-cm diameter entrance, drilled into one end, was covered with tape until 27 April 2009. We checked each tube weekly after opening the tubes: date, presence of nest material, total number and species of eggs present, and number and species of young were recorded at the time of each check. We followed our nest-check protocol through nest completion (presence of young). We did not follow these nests through fledging and data collection ended on 3 August 2009.

We further investigated whether starlings used these newly designed tubes in 2010, assuming any novelty associated with the first year was no
TABLE 1. Species use of 100 27.5-cm length × 9.5-cm inside diameter, polyvinyl chloride (PVC) nest tubes attached horizontally to utility poles at 3 m in height, on the National Aeronautics and Space Administration’s Plum Brook facility in Erie County, Ohio, USA. Each tube had a 5.1-cm diameter entrance. Nesting data were collected from 4 May through 12 August, 2009 and from 21 April through 8 September 2010.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>No. nests</th>
<th>No. clutches depredated</th>
<th>No. nests failing</th>
<th>% Nests fledging young</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern Bluebird</td>
<td>2009</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>Unknown</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>24</td>
<td>1</td>
<td>0</td>
<td>96</td>
</tr>
<tr>
<td>European Starling</td>
<td>2009</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>100</td>
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<tr>
<td></td>
<td>2010</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td>House Sparrow</td>
<td>2009</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>Unknown</td>
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<tr>
<td></td>
<td>2010</td>
<td>18</td>
<td>2</td>
<td>1</td>
<td>98</td>
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<tr>
<td>House Wren</td>
<td>2009</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>Unknown</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>43</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

* Nestlings discovered dead in nest, but no evidence of predation.
* Nests were not monitored through fledging in 2009.

RESULTS

Fifty of the smaller tubes were used for nesting in 2009, 49 by Eastern Bluebirds (Sialia sialis), Tree Swallows (Tachycineta bicolor), or House Wrens (Troglodytes aedon) with one nest unidentified to species (Table 1). Eighty-seven of the smaller tubes were used in 2010 with only two being occupied by a non-native cavity-nesting species. These tubes were occupied by House Sparrows (Passer domesticus) in close proximity to sites where bird seed was provided by an adjacent land owner. Ninety-four percent of the smaller tubes with native species fledged young (Table 1). Starlings were observed sitting on and entering the small tubes in 2009 and 2010, but no evidence of starling nesting was found in either year.

Starlings nested in two of our larger tubes (25\% of occupied tubes) while six of the remaining eight tubes contained nests of Eastern Bluebirds (n = 1 positive identification by egg; 3 possible) and Tree Swallows (n = 2 nests).

DISCUSSION

Our nesting data over two breeding seasons demonstrate successful use of a PVC tube cavity by three native passerine species and avoidance by European Starlings, likely due to a reduced vertical depth. Starlings are recognized as adaptable to a range of cavity dimensions in human structures (Savard and Falls 1981, Feare 1984), but cavity vertical depth may serve as a selective factor in accessible cavities when a variety of cavity dimensions are available. For example, Mazgajski (2003) found that starlings selected nest boxes with a 22-cm vertical depth over similar boxes adjusted to achieve shallower vertical depths, possibly because of benefits in limiting predation. The smaller PVC tubes used in 2009 and 2010 replaced wood nest boxes (28-cm inside length × 12-cm width × 13- to 16-cm vertical distance from floor to sloped ceiling with 5.1-cm entrance) previously used in successive experiments with nesting starlings (Dolbeer et al. 1988, Belant et al. 1998, Seamans et al. 2001, White and Blackwell 2003). Starling use of the wood nest boxes in these studies ranged from 58 to 97% occupancy. McGilvrey and Uhler (1971) reported reduced starling use of 61-cm long × 30.5-cm diameter cylinder Wood Duck (Aix sponsa) tubes mounted horizontally, particularly when the openings exceeded 7.6 cm × 10.2 cm. We speculate that light penetration, lack of clear head space after nest construction or perceived or realized predation risk contributed to the reduced
use of the horizontal tubes. We also found that only 20% of our horizontally-mounted larger tubes (offering >17 cm vertical depth) were used by starlings, whereas native species occupied 60% of these larger tubes.

A variety of factors can influence starling nest cavity selection (McGilvrey and Uhler 1971, Van Balen et al. 1982), and we suggest the 9.5-cm vertical depth of our smaller tubes was a limiting factor for starling use in our study. We believe the smaller tubes could meet the requirements of other native, secondary cavity-nesting passerines and the effects of vertical cavity depth on cavity use by starlings should be further investigated.

ACKNOWLEDGMENTS

Our study was funded by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center. We thank M. E. Conger and D. E. Steyer for field assistance, and E. J. Poggiali for logistical assistance. P. M. Schmidt, L. DeVault, J. T. Tyson, and B. E. Washburn provided reviews of earlier versions of this manuscript.

LITERATURE CITED


Evidence of Medullary Bone in Two Species of Thrushes

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ABSTRACT.—We used micro-computed tomography to examine if medullary bone was present in Wood Thrush (Hylocichla mustelina) and Veery (Catharus fuscescens), two species of Passeriformes. We scanned bones from males and females collected during spring and fall migration, and the breeding season. Medullary bone was found in the humerus, radius-ulna, and tibiotarsi-fibula of a breeding female Wood Thrush and a breeding female Veery, both of which were ovulatory at necropsy. Two other breeding female Wood Thrush, both post-ovulatory at necropsy, did not have medullary bone. We did not observe medullary bone in females collected during spring or fall migration, nor in any males. Our findings support the presence of medullary bone in breeding female passerines, but future studies with larger, targeted sample sizes are needed to examine the phenology of medullary bone formation and resorption, and to explore the extent of medullary bone’s role in eggshell formation in passerines.

Calcium is an essential micronutrient necessary for successful breeding in birds (Perrins 1996) with the majority (98%) of the dry mass of the eggshell being calcium hydroxyapatite, the primary mineral component in bone (Reynolds et al. 2004). Successful egg formation requires adequate dietary calcium, yet little is known about calcium intake, storage, and utilization in wild birds (Reynolds and Perrins 2011). Studies have provided evidence that calcium limitations in wild birds have adverse reproductive consequences (Reynolds and Perrins 2011: table 2.2) including increased eggshell defects, reduced egg size, and incomplete clutches. Evidence suggests females are dependent upon calcium-rich foods in the days leading up to production of an eggshell (Reynolds and Perrins 2011) and generally do not store calcium long-term (Graveland and van Gijzen 2011). However, the possibility of wild birds storing calcium for the short-term in bone, and in particular as medullary bone, remains unclear.

Medullary bone occurs in long bones of some female birds (Kyes and Potter 1934, Zambonin-Zallone and Mueller 1969, Clunies et al. 1992), and its predominant role is as a labile calcium resource that can be used to produce calcified eggshells (Dacke et al. 1993). Medullary bone presence and use as a calcium reservoir for eggshell production is well documented in Galliformes, including Domestic Chickens (Gallus gallus) (Mueller et al. 1964, Zambonin-Zallone and Mueller 1969, Clunies et al. 1992), White-tailed Ptarmigan (Lagopus leucura) (Larison et al. 2001), and Japanese Quail (Coturnix japonica) (van de Velde et al. 1985, Yamamoto and Nagai 1992). Female pigeons (Columbiformes) are known to form medullary bone in preparation for egg-laying (Kyes and Potter 1934). Many of these studies (Kyes and Potter 1934, Zambonin-Zallone and Mueller 1969, van de Velde et al. 1985, Clunies et al. 1992, Yamamoto and Nagai 1992) used histologic techniques to provide direct evidence for the presence of medullary bone.

The presence of medullary bone in other taxa is not well established and, in particular for passerines, the evidence of medullary bone is equivocal. Most studies in passerines have used indirect methods to assay for medullary bone. Evidence including the uptake of radioactive calcium in skeletons of female egg-laying Zebra Finches (Taeniopygia guttata) (Reynolds 1997), and differences in total body calcium in post-laying versus pre-laying and laying female House Sparrows (Passer domesticus) (Krementz and Ankney 1995) suggest the presence of medullary bone. Ankney and Scott (1980) reported heavier leg bones in female Brown-headed Cowbirds (Molothrus ater) about to start laying and laying versus those finishing laying, suggesting the presence of medullary bone. Researchers, using a similar technique, concluded that female Great Tits (Parus major) do not have medullary bone (Graveland and van Gijzen 1994).

Direct evidence for medullary bone presence in
passerines is scarce. We used micro-computed tomography (microCT) (Ruegsegger et al. 1996), to look for medullary bone in wing and leg bones of Wood Thrush (Hylocichla mustelina) and Veery (Catharus fuscens), two species of passerines.

METHODS

Field Collections.—We collected Wood Thrush and Veery during the spring migratory period (24–28 Apr 2005 and 16–30 Apr 2006), near Johnson Bayou in southwest Louisiana, USA (29 45' N, 93 37' W) on the northern coast of the Gulf of Mexico, during the fall migratory period (18 Sep–15 Oct 2005) at Bon Secour National Wildlife Refuge, Fort Morgan Peninsula, Alabama (30 13' N. 88° 10' W), and during the breeding season (24–27 May 2006) at a study site in Lackawanna County, northeastern Pennsylvania (41° 33' N. 75° 43' W). Detailed study site descriptions have been published by Woodrey and Moore (1997) (Fort Morgan Peninsula), Barrow et al. (2000) (Johnson Bayou), and Smith and Hatch (2008) (northeastern Pennsylvania).

We collected the majority of the birds passively using mist nets (12 x 2.6 m with 30-mm mesh). We used a combination of passive and target mist netting techniques at northeastern Pennsylvania to maximize captures and classified males and females in the field by presence of a brood patch or engorged cloacal protuberance. We euthanized birds using CO₂ upon capture and, at necropsy we classified males and females and also recorded any egg formation in the oviduct. All procedures were approved by the Institutional Animal Care and Use Committee at the University of Southern Mississippi (protocol 217-003) and at the University of Scranton (protocol 3-03). Birds were collected under U.S. Fish and Wildlife Service permit MB 758364.

Micro-computed Tomography.—The wing (humerus and radius-ulna) and leg (tibiotarsus-fibula) bones were dissected free of soft tissue in preparation for scanning. The femora were unavailable for dissection due to another ongoing study on body composition (JCO. unpubl. data). We scanned the humerus of each individual using a MicroCT 80 scanning system (μCT 80. Scanco Medical, Basserdorf, Switzerland) at The University of Scranton, which is capable of scanning ex vivo specimens, as part of another ongoing study to examine seasonal differences in bone morphology (MES, unpubl. data). We scanned the radius-ulna and tibiotarsus-fibula when we found medullary bone in the humerus. We also scanned tibiae from an actively laying Domestic Chicken and a broiler chicken as positive and negative controls. We scanned all Wood Thrush and Veery specimens vertically in a cylindrical sample holder (20 mm diam × 65 mm height) at a voltage of 55 kV, intensity of 45 μA, and resolution of 10 μm (isotropic voxel size). The scanning time ranged from 12 to 18 hrs for the humerus, and up to 20–28 hrs for the tibiotarsus-fibula complex. We scanned the chicken bones, because of their larger size, in larger sample holders (35 mm diam × 65 mm height) at a resolution of 18 μm (isotropic voxel size), which took ~30 hrs of scanning time.

We used Scanco Software (Scanco Medical, Basserdorf, Switzerland) to examine two-dimensional (2D) cross sections for presence of medullary bone. We evaluated 2D slices of each bone to create a three-dimensional (3D) image. We drew contour lines around each bone in its entirety prior to evaluation. We applied a Gaussian filter to remove noise from each image followed by segmentation using a single threshold to separate bone from non-bone (marrow and soft tissue). The resultant images were opened in the 3D-viewer and the bones were virtually sliced, making the interior available for examination.

RESULTS

Eight Wood Thrush (4 females and 4 males) and eight Veery (2 females, 5 males, and 1 undetermined) were collected during spring migration (Johnson Bayou), nine Wood Thrush (5 females and 6 males) and nine Veery (1 female and 8 males) were collected during the breeding season (northeastern Pennsylvania), and five Wood Thrush (2 females, 2 males, and 1 undetermined) and two Veery (both males) were collected during fall migration (Fort Morgan Peninsula). We examined these birds as well as an actively laying Domestic Chicken and a broiler chicken (positive and negative control, respectively) for presence of medullary bone. We found no evidence of medullary bone in any females collected during spring or fall migration. In any of the males collected during any season, nor in the broiler chicken (Fig. 1). Medullary bone was present in the laying Domestic Chicken as well as in one (#16) of three female Wood Thrushes and in the female Veery (#10) collected in breeding areas (Fig. 1). Medullary bone was
found in the humerus, radius-ulna (Fig. 2), and tibiotarsus-fibula in both Wood Thrush # 16 and Veery # 10.

The breeding status of females was assigned based on the presence of ovum formation in the oviduct, brood patch, and/or a nest. Wood Thrush # 16 had a fully vascularized brood patch and the nest was also found with four eggs. There was no evidence of ovum formation in the oviduct. Veery # 10 had a fully pigmented egg in the uterus, and two ova were found with only the yolk present. The remaining two Wood Thrush females had no evidence of ovum formation in the oviduct nor had fully vascularized brood patches, indicating they were not incubating eggs.

DISCUSSION

Evidence in the literature of medullary bone in passerines has been equivocal, even in studies that have directly looked for its presence (Ankney and Scott 1980, Pahl et al. 1997, Eeva et al. 2000). Histological analysis of breeding female Great Tits revealed the presence of medullary bone in the tibiotarsus, although it appeared sparse in some bones (Eeva et al. 2000). Medullary bone was found in 80% of pre-laying (without evidence of postovulatory follicles) and 100% of laying (either with oviducal egg or evidence of postovulatory follicles) female Brown-headed Cowbirds examined (Ankney and Scott 1980). However, radiographs of bones from Tree Swallows (Tachycineta bicolor), Brown-headed Cowbirds, and Great Tits demonstrated no difference in leg bone density between pre-laying (collected 9–22 days prior to laying) and post-laying (collected 17–25 days after completion of clutch) females, which suggests an absence of medullary bone (Pahl et al. 1997). A possible confounding factor across these studies, including ours, is when birds were collected relative to the phenology of breeding. For example, both females with medullary bone in our study were collected during ovulation, whereas two female Wood Thrush that did not have medullary bone were post-oviposition. There is increasing support that calcium storage in medullary bone may occur only a few days prior to and disappear shortly after egg laying (Ankney and Scott 1980, Krementz and...
conjunction with its absence in the two post-ovulatory females, breeding males, and migrating males and females supports the hypothesis that these species of passerines, and perhaps all species of passerines as well as other avian Orders, form medullary bone to use as a labile source of calcium during eggshell production (Mueller et al. 1964. Zambonin-Zallone and Mueller 1969, Ankney and Scott 1980, Clunes et al. 1992, Krementz and Ankney 1995).

We found medullary bone in the long bones of female Wood Thrush and Veery during a period when these females were forming eggs. We did not observe medullary bone in post-ovulatory females, males, or in female birds collected during other, non-breeding phases of the avian annual cycle. Our study was unique in that it used micro-computed tomography to directly image medullary bone in these specimens. We hypothesise that absence of medullary bone in passerine females in this and other studies (Ankney and Scott 1980, Pahl et al. 1997, Ecva et al. 2000) may be a consequence of when birds were collected during the breeding season. Studies that actively target a larger number of females throughout the breeding season, permitting a more in-depth examination of the timeline of medullary bone formation and resorption in passerines, are required to evaluate this assumption. Future studies are needed to explore the extent of the role medullary bone has in eggshell formation in passerine birds.

ACKNOWLEDGMENTS

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LITERATURE CITED
Vocal Distinctiveness and Information Coding in a Suboscine with Multiple Song Types: Eastern Wood-Pewee

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ABSTRACT.—We tested individual distinctiveness, a prerequisite for individual recognition, in the songs of the suboscine Eastern Wood-Pewee (Contopus virens). Male Eastern Wood-Pewees produce two main song types: 'pee-ah-wee' and 'wee-ooo' songs. All song variables for both song types, including temporal and frequency variables, showed greater between than within individual variation. Thus, both song types contained the potential to code information on individual identity and quality. Pee-ah-wee songs were more variable than wee-ooo songs, and pee-ah-wee frequency variable measures were the most variable. We correctly assigned 97.5% of pee-ah-wee songs and 95.0% of wee-ooo songs to the bird of origin—demonstrating individual distinctiveness in both main song types.

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variables for both song types, including temporal and frequency variables, showed greater between than within individual variation. Thus, both song types contained the potential to code information on individual identity and quality. Pee-ah-wee songs were more variable than wee-ooo songs, and pee-ah-wee frequency variable measures were the most variable. We correctly assigned 97.5% of pee-ah-wee songs and 95.0% of wee-ooo songs to the bird of origin—demonstrating individual distinctiveness in both main song types. Received 14 March 2011. Accepted 27 June 2011.
Numerous studies demonstrate that oscine songs are individually distinctive and can be used to identify individuals based on song alone. However, relatively little is known about songs of suboscines, particularly individual distinctiveness (Lovell and Lein 2004). Subosine songs are generally thought to be less variable than those of oscines as they are not learned (Kroodsma 1984), which leaves less chance for errors in the learning process (Raposo and Hörling 2003, Wiley 2005). Reduced variability could diminish the ability of songs of suboscines to provide information on individual identity and quality or geographic population structure.

Several recent studies have explored subosine song distinctiveness, song discrimination, and even individual recognition (e.g., Sedgewick 2001, Bard et al. 2002, Rios-Chelén et al. 2005, Wiley 2005, Fitzsimmons et al. 2008, Lein 2008, Fernández-Juricic et al. 2009). Lovell and Lein (2004) demonstrated the subosine Alder Flycatcher (Empidonax alnorum) could discriminate between the songs of neighbors versus strangers and that this species was also capable of individual recognition via vocalizations alone (Lovell and Lein 2005), the first time this ability was shown in a subosine.

We explored vocal distinctiveness in the Eastern Wood-Pewee (Contopus virens), a subosine of eastern North America (McCarty 1996) with several distinct male songs, including the onomatopoeic ‘pee-ah-wee’ song, for which this species is named, as well as this species’ main secondary vocalization, the ‘wee-ooo’ song. Ornithologists have long focused on Eastern Wood-Peeee songs (e.g., Craig 1943, Smith 1988), although studies of this species’ songs have not explored individual distinctiveness.

Vocalizations should have relatively little within individual variation to effectively convey information while being comparatively more variable between individuals (Falls 1982). The production of a unique set of vocalizations by an individual constitutes a vocal signature. Our objective was to test our prediction that both the pee-ah-wee and wee-ooo songs of male Eastern Wood-Pewees contain individually-specific vocal signatures.

**METHODS**

We recorded pee-ah-wee and wee-ooo songs produced by male Eastern Wood-Pewees under natural conditions in Westchester County, New York and Fairfield County, Connecticut, USA during early June 2008. We used a Marantz PMD660 digital recorder with a Sennheiser ME66 directional microphone to record songs. We visually tracked focal birds, and all songs of each focal male were recorded in a single recording session to ensure all recordings were of focal males. We ended the recording session and all recordings from that session were excluded from analyses if we lost visual contact with a focal individual or another conspecific individual appeared. We recorded and analyzed 323 pee-ah-wee songs from 16 males and 201 wee-ooo songs from 17 males. Songs of individuals could vary over time or with motivational circumstances. Our method is unlikely to capture such variation.

Songs were digitized at a sampling rate of 22.05 kHz and a 16-bit depth, and presented as spectrograms generated with FFT of 1,024 and a Hamming window using Syrinx sound analysis software (John Burt, www.syrinxpc.com). We selected a maximum of 20 pee-ah-wee and wee-ooo songs for each focal male, choosing recordings with the highest signal-to-noise ratio. We measured or calculated temporal, spatial proportion, frequency, and frequency modulation variables for each song type using cursors on each spectrogram displayed on a computer screen (Tables 1 and 2; Fig. 1). Measurement variables were examined to confirm assumptions of normality and equality of variance were met.

Spectrograms represent a trade-off between precision in temporal and frequency measures. We elected to use a single spectrogram for both temporal and frequency measures to greatly reduce the number of individual measurements required. For example, a single placement of cursors on the computer screen can provide simultaneous measurements of duration, as well as starting, ending, minimum, and maximum frequencies. Any loss of precision could reduce our ability to detect small differences within and between individual song variables. However, the relative tonal clarity and brevity of pee-ah-wee and wee-ooo song traces on the spectrograms somewhat minimize the loss of measurement precision as compared to acoustic sounds that cover larger frequency bands and are longer.

We calculated a value, the ‘potential for information coding’ (PIC), for all song measurements to evaluate and compare the within and between individual variation of both pee-ah-wee
TABLE 1. Mean ± SD and potential for information coding (PIC) values for 25 variables measured for 20 pee-ah-wee songs for 16 male Eastern Wood-Pewees. T = temporal measures (sec); TP = temporal proportion measures; F = frequency measures (kHz); and FM = frequency modulation measures (kHz). CV_b = between individual coefficient of variation; CV_w = within individual coefficient of variation. PIC = CV_b/CV_w.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean ± SD</th>
<th>F_b, kHz</th>
<th>CV_b</th>
<th>CV_w</th>
<th>PIC</th>
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<tbody>
<tr>
<td>T1 (A to G)</td>
<td>1.18 ± 0.16</td>
<td>136.6</td>
<td>13.31</td>
<td>4.66</td>
<td>2.9</td>
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<tr>
<td>T2 (A to C)</td>
<td>0.12 ± 0.02</td>
<td>264.5</td>
<td>17.68</td>
<td>5.08</td>
<td>3.5</td>
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<tr>
<td>T3 (D to F)</td>
<td>0.29 ± 0.07</td>
<td>315.9</td>
<td>24.24</td>
<td>6.06</td>
<td>4.0</td>
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<td>T4 (F to G)</td>
<td>0.77 ± 0.16</td>
<td>137.3</td>
<td>21.31</td>
<td>7.85</td>
<td>2.7</td>
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<td>T5 (A to B)</td>
<td>0.07 ± 0.01</td>
<td>67.4</td>
<td>20.70</td>
<td>9.33</td>
<td>2.2</td>
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<td>T6 (B to C)</td>
<td>0.04 ± 0.01</td>
<td>52.9</td>
<td>21.64</td>
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<td>T7 (D to E)</td>
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<td>T8 (E to F)</td>
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<td>30.49</td>
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<td>T9 (B to E)</td>
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<td>25.17</td>
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<td>NA</td>
<td>23.56</td>
<td>9.93</td>
<td>2.4</td>
</tr>
<tr>
<td>T11 (T2/T1)</td>
<td>NA</td>
<td>NA</td>
<td>22.27</td>
<td>6.47</td>
<td>3.4</td>
</tr>
<tr>
<td>F1 (A)</td>
<td>3.46 ± 0.24</td>
<td>83.9</td>
<td>6.88</td>
<td>2.93</td>
<td>2.3</td>
</tr>
<tr>
<td>F2 (B)</td>
<td>4.55 ± 0.24</td>
<td>360.2</td>
<td>5.30</td>
<td>1.15</td>
<td>4.6</td>
</tr>
<tr>
<td>F3 (C)</td>
<td>3.35 ± 0.20</td>
<td>184.8</td>
<td>5.92</td>
<td>1.80</td>
<td>3.3</td>
</tr>
<tr>
<td>F4 (D)</td>
<td>3.62 ± 0.27</td>
<td>306.4</td>
<td>7.35</td>
<td>1.76</td>
<td>4.2</td>
</tr>
<tr>
<td>F5 (E)</td>
<td>4.81 ± 0.30</td>
<td>357.4</td>
<td>6.17</td>
<td>1.37</td>
<td>4.5</td>
</tr>
<tr>
<td>F6 (F)</td>
<td>3.37 ± 0.20</td>
<td>545.7</td>
<td>6.09</td>
<td>1.14</td>
<td>5.3</td>
</tr>
<tr>
<td>F7 (G)</td>
<td>4.05 ± 0.28</td>
<td>224.2</td>
<td>7.03</td>
<td>2.01</td>
<td>3.5</td>
</tr>
<tr>
<td>F11 (A to B)</td>
<td>1.08 ± 0.20</td>
<td>43.1</td>
<td>18.82</td>
<td>10.88</td>
<td>1.7</td>
</tr>
<tr>
<td>F12 (B to C)</td>
<td>1.19 ± 0.21</td>
<td>153.9</td>
<td>17.98</td>
<td>5.94</td>
<td>3.0</td>
</tr>
<tr>
<td>F13 (D to E)</td>
<td>1.19 ± 0.33</td>
<td>277.5</td>
<td>28.06</td>
<td>7.67</td>
<td>3.7</td>
</tr>
<tr>
<td>F14 (E to F)</td>
<td>0.68 ± 0.22</td>
<td>245.3</td>
<td>18.85</td>
<td>4.98</td>
<td>3.8</td>
</tr>
<tr>
<td>F15 (F to G)</td>
<td>0.68 ± 0.22</td>
<td>123.5</td>
<td>32.85</td>
<td>13.57</td>
<td>2.4</td>
</tr>
<tr>
<td>F16 (G to A)</td>
<td>0.64 ± 0.28</td>
<td>71.8</td>
<td>43.04</td>
<td>23.60</td>
<td>1.8</td>
</tr>
<tr>
<td>F17 (A to E)</td>
<td>1.34 ± 0.28</td>
<td>90.4</td>
<td>20.67</td>
<td>9.31</td>
<td>2.2</td>
</tr>
</tbody>
</table>

*F-values for one-way ANOVAs comparing between and within individual variation for each song variable: all P < 0.0001.*
TABLE 2. Mean ± SD and potential for information coding (PIC) values for 25 variables measured for five to 20 wee-oo songs for 17 male Eastern Wood-Pewees. T = temporal measures (sec); TP = temporal proportion measures; F = frequency measures (kHz); and FM = frequency modulation measures (kHz). CV_b = between individual coefficient of variation; CV_w = within individual coefficient of variation. PIC = CV_w/CV_b.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean ± SD</th>
<th>F_{bonf}{\text{*}}</th>
<th>CV_b</th>
<th>CV_w</th>
<th>PIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>T1 (A to F)</td>
<td>0.96 ± 0.15</td>
<td>97.8</td>
<td>15.78</td>
<td>5.24</td>
<td>3.0</td>
</tr>
<tr>
<td>T2 (A to C)</td>
<td>0.38 ± 0.05</td>
<td>83.3</td>
<td>12.95</td>
<td>4.60</td>
<td>2.8</td>
</tr>
<tr>
<td>T3 (C to E)</td>
<td>0.10 ± 0.01</td>
<td>24.6</td>
<td>13.31</td>
<td>6.69</td>
<td>2.0</td>
</tr>
<tr>
<td>T4 (E to F)</td>
<td>0.48 ± 0.13</td>
<td>76.6</td>
<td>27.25</td>
<td>9.75</td>
<td>2.8</td>
</tr>
<tr>
<td>T5 (A to B)</td>
<td>0.18 ± 0.03</td>
<td>28.9</td>
<td>16.21</td>
<td>8.12</td>
<td>2.0</td>
</tr>
<tr>
<td>T6 (B to C)</td>
<td>0.20 ± 0.04</td>
<td>98.7</td>
<td>17.79</td>
<td>6.48</td>
<td>2.7</td>
</tr>
<tr>
<td>T7 (C to D)</td>
<td>0.04 ± 0.01</td>
<td>4.5</td>
<td>29.08</td>
<td>5.88</td>
<td>2.0</td>
</tr>
<tr>
<td>T8 (D to E)</td>
<td>0.06 ± 0.01</td>
<td>13.3</td>
<td>16.50</td>
<td>6.69</td>
<td>2.0</td>
</tr>
<tr>
<td>T9 (B to D)</td>
<td>0.24 ± 0.04</td>
<td>59.3</td>
<td>16.36</td>
<td>6.64</td>
<td>2.5</td>
</tr>
<tr>
<td>TP1 (T2-T6/T1)</td>
<td>NA</td>
<td>NA</td>
<td>17.99</td>
<td>8.93</td>
<td>2.0</td>
</tr>
<tr>
<td>TP2 (T2/T1)</td>
<td>NA</td>
<td>NA</td>
<td>15.14</td>
<td>6.29</td>
<td>2.4</td>
</tr>
<tr>
<td>TP3 (T2 + T7/T1)</td>
<td>NA</td>
<td>NA</td>
<td>14.73</td>
<td>6.62</td>
<td>2.3</td>
</tr>
<tr>
<td>F1 (A)</td>
<td>3.21 ± 0.20</td>
<td>21.8</td>
<td>6.33</td>
<td>3.74</td>
<td>1.7</td>
</tr>
<tr>
<td>F2 (B)</td>
<td>4.72 ± 0.26</td>
<td>244.1</td>
<td>5.46</td>
<td>1.12</td>
<td>4.9</td>
</tr>
<tr>
<td>F3 (C)</td>
<td>3.80 ± 0.16</td>
<td>97.1</td>
<td>4.07</td>
<td>1.36</td>
<td>3.0</td>
</tr>
<tr>
<td>F4 (D)</td>
<td>6.20 ± 0.50</td>
<td>64.3</td>
<td>8.10</td>
<td>2.99</td>
<td>2.7</td>
</tr>
<tr>
<td>F5 (E)</td>
<td>3.24 ± 0.12</td>
<td>77.0</td>
<td>3.58</td>
<td>1.29</td>
<td>2.8</td>
</tr>
<tr>
<td>F6 (F)</td>
<td>2.78 ± 0.17</td>
<td>25.0</td>
<td>6.05</td>
<td>3.47</td>
<td>1.7</td>
</tr>
<tr>
<td>FM1 (A to B)</td>
<td>1.51 ± 0.27</td>
<td>34.9</td>
<td>18.02</td>
<td>9.01</td>
<td>2.0</td>
</tr>
<tr>
<td>FM2 (B to C)</td>
<td>0.92 ± 0.23</td>
<td>170.3</td>
<td>25.15</td>
<td>6.93</td>
<td>3.6</td>
</tr>
<tr>
<td>FM3 (C to D)</td>
<td>2.41 ± 0.48</td>
<td>61.2</td>
<td>20.12</td>
<td>7.61</td>
<td>2.6</td>
</tr>
<tr>
<td>FM4 (D to E)</td>
<td>2.96 ± 0.54</td>
<td>77.1</td>
<td>18.31</td>
<td>6.08</td>
<td>3.6</td>
</tr>
<tr>
<td>FM5 (E to F)</td>
<td>0.45 ± 0.13</td>
<td>10.3</td>
<td>28.57</td>
<td>23.56</td>
<td>1.2</td>
</tr>
<tr>
<td>FM6 (A to F)</td>
<td>0.43 ± 0.18</td>
<td>10.9</td>
<td>42.80</td>
<td>39.25</td>
<td>1.1</td>
</tr>
<tr>
<td>FM7 (D to F)</td>
<td>3.42 ± 0.55</td>
<td>56.7</td>
<td>16.18</td>
<td>6.42</td>
<td>2.5</td>
</tr>
</tbody>
</table>

* F-values for one-way ANOVAs comparing between and within individual variation for each song variable; all P < 0.0001.

Thus, the song being classified is not used to both develop the linear function and to test that function. We used one-way ANOVAs to compare within and between individual variation for each song variable. We conducted all statistical testing using SPSS Version 17 statistical software (SPSS 2008).

RESULTS

All 25 variables measured for pee-ah-wee and wee-oo songs had PIC values >1 (Tables 1, 2). PIC values for pee-ah-wee song variables were similar for temporal and frequency modulation measures but higher for frequency measures (ANOVA: F_{2,20} = 5.21, P = 0.01; Tukey HSD post-hoc test) (Table 1). PIC values were similar for all wee-oo song variable categories (ANOVA: F_{2,19} = 0.74, P = 0.49) (Table 2). The sample of temporal proportion measures was too small for comparative analysis, PIC values were higher for pee-ah-wee than wee-oo songs when all variables were combined (t-test: t_{47} = 2.62, P = 0.01).

Principal component analysis of the 25 pee-ah-wee song variables generated six principal components with eigenvalues >1.0 that explained 88.4% of the variance. We used those principal components as the basis for a discriminant function analysis and correctly assigned 97.5% of pee-ah-wee songs (315/323) to the correct individual. Principal component analysis of the 25 wee-oo song variables generated seven principal components with eigenvalues >1.0 that explained 88.9% of the variance. We used those principal components as the basis for a discriminant function analysis and correctly assigned 95.0% of wee-oo songs (191/201) to the correct individual.

DISCUSSION

Each recent study of suboscine song, including ours, found sufficient variability to demonstrate
(A) Pee-ah-wee Song

FIG. 1. Spectograms of the two main song types of the Eastern Wood-Pewee: (A) Pee-ah-wee and (B) Wee-ooo. Capital letters show inflection points used to measure call variables.

(B) Wee-ooo Song

geographical variation, individual distinctiveness, or individual identification (Fitzsimmons et al. 2008). Our results indicate both pee-ah-wee and wee-ooo songs in male Eastern Wood-Pewees have the potential to code information and contain individually-specific signatures. Why pee-ah-wee songs are more variable than wee-ooo songs and why pee-ah-wee frequency measures are the most variable of the song variables we measured is unclear and requires further testing. The function of multiple song types in suboscines is almost entirely unknown (Smith 1988) and requires further study.

Individual distinctiveness in multiple song types in a subscine has been shown in only one other species: the Buff-breasted Flycatcher (Empidonax fulvifrons) (Lein 2008). Lein (2008) did not explicitly calculate PIC values for Type 1 and Type 2 Buff-breasted Flycatcher songs. However, Lein (2008, tables 4 and 5) presented values for both CVw and CVb, for song variables measured—allowing us to calculate PIC values. We did not conduct statistical analyses of the PIC values calculated from Lein (2008); but, on visual inspection, PIC values calculated appear consistent with those we calculated for Eastern Wood-Pewee songs. The variable with the highest PIC value in Lein’s (2008) and our study was a frequency measure. PIC values have the potential to allow comparison of variability not only within species, but also between species. Additional data from more suboscines are needed to better understand variability and distinctiveness in subscine song.

ACKNOWLEDGMENTS

The Louis Calder Center—Biological Field Station of Fordham University, Teatown Lake Reservation, Audubon Greenwich, and Westmoreland Sanctuary provided access to field sites for this study. The Calder Summer Undergraduate Research Program at Fordham University provided funding to Justina Leung.

LITERATURE CITED


Affinities of Three Vagrant Cave Swallows from Eastern North America

Joshua I. Engel,1,3 Mary H. Hennen,1 Christopher C. Witt,2 and Jason D. Weckstein1

ABSTRACT.—We analyzed the mitochondrial cytochrome b gene of three vagrant Cave Swallow (Petrochelidon fulva) specimens from Illinois, New York, and New Jersey and compared them to published sequences from across the breeding range of the species. All three specimens were assigned to the southwestern United States/Mexico subspecies (P. f. pallida group) on the basis of plumage coloration. Molecular results reveal that all three birds possess unique and novel mitochondrial haplotypes that are closely related to haplotypes from known P. f. pallida individuals. None of the three haplotypes from the vagrant individuals is within the monophyletic clade of haplotypes that corresponds to the Caribbean subspecies (P. f. fulva).

Received 27 January 2011. Accepted 8 July 2011.

The expansion in breeding and wintering range of the Cave Swallow (Petrochelidon fulva) has coincided with a dramatic increase in vagrant birds far to the east and north of their normal range, particularly in autumn. Several have been found dead and these specimens deposited in museum collections. The origins of these vagrants are not always clear due to difficulties with identification. Identifying these vagrants with certainty using genetic methods can help unravel the poorly understood relationship between vagrancy and breeding range expansion. Genetic methods have been previously used to identify vagrant birds to species (e.g., Thorup et al. [2009] identified two Phylloscopus warblers and Witt et al. [2010] identified a Brachyramphus murrelet), but this is the first attempt to do so at the population level.

The Cave Swallow, according to mitochondrial DNA (mtDNA) data (Kirchman et al. 2000), consists of two diagnosable forms, one breeding in the Greater Antilles and Florida (P. f. fulva group) and the other breeding in the southwestern United States and Mexico (P. f. pallida group: West [2005]; nomenclature follows AOU [2000]). Most specimens are diagnosable via plumage coloration patterns, but field identification of the two forms is extremely difficult.

Previous specimen records of vagrant Cave Swallows in eastern North America have primarily been identified as P. f. pallida, including autumn specimens from New York, New Jersey, Ontario, South Carolina, Virginia, and Ohio (McNair and Post 1999, Dinsmore and Farnsworth 2006, Spahn and Tetlow 2006, O’Brien 2007, Post 2008). There are winter specimens from South
SHORT COMMUNICATIONS

Carolina of *P. f. pallida* and an autumn specimen from Missouri in 1977 that was identified by measurements and plumage as *P. f. fulva* (Easterla 2008). There are also recent spring records from eastern North America (c.g.. Massachusetts [SzantvvlOlO]; and Ontario [Wormington 2010]).

A Caw Swallow collided with a window at McCormick Place (41° 51.308’ N, 87° 36.770’ W ± 8 ml on 10 November 2008 along the Chicago, Illinois lakefront and was found dead by MHH and deposited at the Field Museum of Natural History (FMNH). The bird was prepared as a study skin (FMNH 461103) and a tissue sample was taken (MCP08-625). Multiple Cave Swallows were found dead at the Cape May Congress Hall, Cape May, New Jersey (38° 55.856’ N, 74° 55.469’ W ± 100 m) on 27 November 2007 (O’Brien 2007). One of these birds was deposited at the University of New Mexico’s Museum of Southwestern Biology (MSB 29350), prepared as a study skin with partial skeleton (ABJ 2455), and a tissue sample was taken (NK170651). Our objectives, based on these specimens, were to (1) identify the specimens to subspecies based on morphology and genetics, and (2) consider the identifications in terms of expanding populations and vagrancy.

**METHODS**

We sequenced a portion of the mtDNA cytochrome *b* (cyt *b*) gene of each specimen to independently assess their identification and geographic origins with respect to the mtDNA data set previously published by Kirchman et al. (2000). We also included data recently published (Dor et al. 2010) from a vagrant Cave Swallow salvaged in New York and, to increase our sample size of breeding birds, we sequenced one additional Cave Swallow from Valverde County, Texas (MSB 18680).

We extracted total genomic DNA from two vagrant (FMNH 461103 and MSB 29350) and one breeding (MSB 18680) Cave Swallow using the DNeasy tissue extraction kit (Qiagen, Valencia, CA, USA) following the manufacturer’s protocols. We used primers L.14841 (all 3 samples; Kocher et al. 1989), H316065 (FMNH sample; Helm-Bychowski and Cracraft 1993), and H4a (MSB samples; Harshman 1996) to amplify and directly sequence a portion of the mtDNA cyt *b* gene. We followed Putel et al. (2011) for thermal cycling, visualization, and sequencing protocols for the FMNH sample. Cytochrome *b* for the MSB samples was amplified in 15 μl reactions using 2 μl of the DNA extract and the following reagents: 0.15 μl of Taq Gold polymerase (ABI, Mountain View, CA, USA), 200 μM of each dNTP, 1.5 mM MgCl₂, and 0.5 μM of each primer. Eppendorf Mastercycler (Eppendorf, Hamburg, Germany) thermal-cyclers were used to conduct the following PCR protocol: 95° for 8 min, (95° for 30 sec, 50° for 30 sec, 72° for 60 sec) × 35 cycles, and 72° for 10 min. PCR products were visualized on 1% agarose gel and cleaned using ExoSAP-IT (USB, Cleveland, OH, USA). Sequencing reactions with external primers used BigDye 3.1 chemistry (Applied Biosystems, Foster City, CA, USA) and were visualized using an ABI 3130 automated sequencer. We assembled the sequences and inspected chromatograms manually using Sequencher 4.7 (at MSB) and 4.10.1 (at FMNH; Gene Codes Corp., Ann Arbor, MI, USA).

We aligned 921 bp of these sequences (Genbank accession #s JN227534–JN227536) with sequences deposited in Genbank by Kirchman et al. (2000) (accession #s AF182379–182391) and Dor et al. (2010) (accession # GU460285) using Sequencher 4.10.1 (Gene Codes Corp., Ann Arbor, MI, USA). Sequences from Kirchman et al. (2000) were taken from breeding colonies throughout the Cave Swallow’s breeding range; the Dor et al. (2010) specimen was an autumn vagrant found dead on 19 November 2005 in Tompkins County, New York (Cornell University Museum of Vertebrates 51713).

We generated a 95% statistical parsimony haplotype network using TCS Version 1.21 (Clement et al. 2000). We used PAUP* (Version 4.0b10; Swofford 2003) to construct a maximum parsimony tree using a heuristic search with TBR branch swapping and 100 random addition replicates. Support for nodes was estimated by 1,000 bootstrap replicates with one random addition per replicate. PAUP* was also used to calculate uncorrected *p*-distances. We conducted a Bayesian analysis using MrBayes 3 (Ronquist and Huelsenbeck 2003) and used a general-time-reversible model of sequence evolution incorporating parameters for invariable sites and gamma rate heterogeneity. All parameters were estimated as part of the analysis and we conducted two parallel runs, each with four Markov chains and for 5 million generations. We sampled the Markov chains every 500 generations and used these 10,000 parameter point estimates minus the burn-in (500 generations) to create a 50% majority rule.
RESULTS

Both the Illinois and New Jersey Cave Swallows show a pale buffy throat, relatively pale cinnamon rump and forehead, and lack extensive rufous on the flanks that distinguish P. f. pallida from P. f. fulva. However, the New Jersey specimen has several fresh, sheathed feathers growing in on the rump that are strikingly darker (chestnut) than the existing, pale orange-cinnamon rump feathers (photograph at http://arctos.database.museum/guid/MSB:Bird;29350). This coloration is due to wear and underscores the difficulty of subspecies identification by plumage alone. The Illinois specimen has a wing measurement of 104 mm and tail measurement of 44 mm. The New Jersey specimen has highly asymmetrical wing measurements (right wing 107 mm, left wing 102 mm) and a tail measurement of 49 mm.

The Illinois and New Jersey specimens were both females with 100% skull ossification and ovaries measuring $4 \times 2$ mm (finely granular), and $2 \times 3$ mm, respectively. Both are hatch-year birds, as indicated by suspended wing molt, with primaries 5–9 (IL) and primaries 4–9 (NJ) and the corresponding primary coverts relatively worn and pale, and primaries 1–4 (IL) and primaries 1–3 (NJ) fresh and dark.

The Illinois, New Jersey, and New York Cave Swallow haplotypes are each unique and different from one another and from the breeding specimens of P. f. pallida from Tom Green County, Texas. The Illinois specimen is one base pair different from both Texas haplotypes (uncorrected $p$-distance of 0.1%: Table 1). The New Jersey specimen is three to five base pairs different from the Texas haplotypes (0.3–0.5%), and the New York specimen is one to four base pairs different from the Texas haplotypes (0.1–0.4%). The shortest number of steps between any P. f. pallida and a member of the P. f. fulva clade is five (Valverde County, Texas to Cuba; Fig. 1). All three vagrants, based on uncorrected cyt $b$ $p$-distances, are genetically closer to previously published breeding P. f. pallida than to breeding P. f. fulva (Table 1).

The Bayesian analysis supports the monophyly of the P. f. fulva group (Bayesian posterior probability = 0.97; Fig. 2), to the exclusion of the three vagrants. Bootstrap support for the P. f. fulva group is relatively weak (57%) because of the small number of informative characters among these recently diverged haplotypes. Neither analytical method provides strong statistical support for the monophyly of P. f. pallida. Thus, the exact position of the vagrant samples with respect to Caribbean and Texas/Mexico birds is unclear.

DISCUSSION

Both the Illinois and New Jersey Cave Swallows, based on plumage characteristics, can be assigned to the P. f. pallida group, although the potential for color changes due to plumage-wear makes this identification tentative. Wing and tail measurements of the Illinois specimen, as well as wing measurements of the New Jersey specimen were in the area of overlap between the two subspecies groups, but the tail measurement of the specimen from New Jersey was outside the range of P. f. fulva but within the range of P. f. pallida.
Fig. 1. Haplotype network of all *P. fulva* samples in the study showing two clusters, one for each subspecies group. Each line represents a single mutational step with solid circles indicating unsampled haplotypes. The dashed line indicates the division between *P. fulva* subspecies groups. The size of each circle is proportional to the total number of samples with the corresponding haplotype and the number in parentheses indicates the number of samples carrying that haplotype from a given location.

Based on the measurements presented by West (1995), Kirchman et al. (2000), using mtDNA cyt b data, found strong bootstrap support (79% for each clade in a maximum parsimony analysis) for the reciprocal monophyly of *P. f. pallida* and *P. f. fulva*. The addition of the sequences from the Illinois, New Jersey, and New York vagrants caused an unexpected breakdown of reciprocal monophyly (Fig. 2). However, the haplotype network shows clear affinities of all three vagrants to *P. f. pallida* (Fig. 1), despite all three vagrants as well as the newly-added Texas specimen having mtDNA haplotypes that differ from those published by Kirchman et al. (2000). That these three individuals carried previously unsampled haplotypes suggests they may have originated from populations other than those sampled by Kirchman et al. (2000), although it is possible that sampling more individuals may have revealed these haplotypes.

A combination of plumage, genetic distances, haplotype network, and the Bayesian support for the *P. f. fulva* group are consistent with the vagrant Cave Swallow specimens having originated from the *P. f. pallida* populations of the southwestern USA or Mexico. This evidence reaffirms the putative link between rapid population expansion and the spate of vagrancy in this species over the past two decades.

ACKNOWLEDGMENTS

We thank David Willard for providing the FMNH tissue sample and the Cape May Bird Observatory, Richard
FIG. 2. Maximum parsimony bootstrap tree of all *P. fulva* samples examined. Bootstrap values $>70\%$ are shown above the nodes and Bayesian posterior probabilities $>0.95$ are shown below the nodes. Samples in bold indicate sequences new to this study. Sample numbers are tissue numbers from Kirchman et al. (2000) or specimen numbers (new sequences). ANSP = Academy of Natural Sciences, Philadelphia; CUMV = Cornell University Museum of Vertebrates; FMNH = Field Museum of Natural History, Chicago; MSB = Museum of Southwestern Biology, University of New Mexico; LSU =...
Crossley, Debra Crossley, Matthew Graus, Andrew Johnston, Sabrina McNew, Michael O'Brien, and Louise Zemlins for providing the New Jersey specimen and associated data to CCW and the MSB. This study was supported in part by NSF DEB-0515672 to JDW and the Field Museum’s Emerging Pathogens Project, funded by the Davee Foundation and the Dr. Ralph and Marian Falk Medical Research Trust. JIB was supported by a grant from the John D. and Catherine T. MacArthur Foundation.

LITERATURE CITED


Eastern Screech-Owl Catches Fish By Wading

Vladimir Dinets

ABSTRACT.—I observed an Eastern Screech-Owl (Megascops asio) wading to catch fish in a small lake in the Everglades, Florida, USA. This fishing technique has not been recorded previously in this species or in other small owls. Received 11 March 2011. Accepted 20 May 2011.

Eastern Screech-Owls (Megascops asio) are known to capture fish by flying from a perch or hopping from shore (Prescott 1985, Gehlbach 1994), but apparently have not been observed wading to catch fish. I observed an Eastern Screech-Owl catching fish by wading at Clearwater Slough in Big Cypress National Preserve, Florida during a 6-year study of crocodilian behavior that included extensive night-time observations.

OBservations

Clearwater Slough (25° 47' 19" N, 81° 06' 00" W) is a body of water ~500 m² in size, up to 2 m deep, and is surrounded by seasonally flooded bald cypress (Taxodium distichum) forest. It has water current for most of the year but is stagnant in spring, when water levels are lowest. I conducted observations at the slough from 1 April until 15 May 2006, 3 days a week, from 1 hr before sunset until 3 hrs after sunrise, from a car parked on a bridge. Full moons occurred on 14 April and 13 May.

I observed a gray-morph Eastern Screech-Owl on three consecutive nights starting 11 May 2006. The bird was walking slowly along the edge of the slough, at times wading into the water up to 30 cm from the shore, to the depth of ~3 cm. I observed it for 5 min on the first night starting at 0312 hrs EDT. It caught a fish ~3 cm long and immediately flew away. On another night I watched it for 12 min starting at 0405 hrs. It flushed after a 1.5-m long American alligator (Alligator mississippiensis) approached it to within 1 m. On a third night I observed it for less than 1 min at 0304 hrs. It caught a fish ~5 cm long, flew to a small branch ~60 cm above the water and, after perching there for <1 min with the fish in its talons, flew out of sight. Both fish were caught by a rapid movement of one foot. They could not be identified, but the shallow area where the owl waded was frequented by introduced sailfin mollies (Poecilia latipinna).

In April 2007, a Barred Owl (Strix varia) was repeatedly seen fishing in the same way at the same location.

Discussion

Fishing has been reported for many large owls (Marks et al. 1999), but there seem to be few published observations of fishing behavior by small owls. The only other small owls known to fish are the closely related Western Screech-Owl (M. kennicottii), which has been observed catching crayfish and fish by flying from a perch (Cannings and Angell 2001), and the Vermiculated Screech-Owl (M. guatemalae), which had fish in stomach contents (Land 1970). This lack of data might reflect the uniqueness of these three species’ fishing abilities among small owls or, more likely, poor knowledge of foraging behavior of many small owls. Eastern Screech-Owls use all fishing techniques known (Marks et al. 1999) for owls: wading (present study), flying from a perch (Prescott 1985), and hopping from shore (Gehlbach 1994).

The timing of the fishing activity seems unusual, as screech-owls are more active during the first half of the night (Johnsgard 1988). The slough at the time of observation had rapidly decreasing water levels and high fish density, and was attracting many other fish-eaters. Up to 15 Black-crowned Night-Herons (Nycticorax nycticorax), five Yellow-crowned Night-Herons (Nyctanassa violacea), 12 Great Blue Herons (Ardea herodias), 12 Great Egrets (A. alba), and 2–3 Wood Storks (Mycteria americana) were present there at night. Black-crowned Night-Herons were replaced at dawn by up to 30 White Ibises (Eudocimus albus), a number of smaller egrets and, on most days, by five resident North American otters (Lontra canadensis). Eight
American alligators were also actively fishing and courting there from sunset until 1–2 hrs after midnight. Fishing activity by these species was not recorded in detail, but the owl apparently visited the slough when the number of individuals of other bird species was lowest, between a rush of activity by larger birds during the first half of the night and another peak in activity at dawn.

LITERATURE CITED


William and Nancy Klamm Service Award for 2011:
Charles and Leann Blem
The Wilson Ornithological Society, like most scientific societies, relies upon the contributions of countless volunteers who participate in committees, review articles, and serve as officers and council members. Without people who are willing to contribute in a myriad of ways, our societies would not move forward, our journals would not be published, and our grants would not be awarded. This year, we are pleased to present the Klamm Service Award to a couple who generously served the Wilson Ornithological Society for more than two decades, and who have had lasting impacts both on the society and on ornithology through their contributions.

Charles and Leann Blem have been an amazing team in all aspects of their lives. This husband and wife team taught together, worked together on studies of Prothonotary Warbler (Protonotaria citrea) breeding biology, and served the Wilson Ornithological Society together. In 1987, Charlie was elected Editor of the Wilson Bulletin, a position he held for 10 years. During his tenure, submissions to the Wilson Bulletin increased and Charlie was able to improve the quality of the journal by being more selective in the articles he accepted. As an editor, Charlie tried to be honest but constructive and encouraging with his criticism. His supportive approach to the publication process encouraged and often mentored authors, especially new authors; thus, Editor Blem helped launch the careers of many ornithologists whose first foray into publication was in the Wilson Bulletin. Charlie could not have handled that task alone and, from the beginning, Leann served as an Assistant Editor for the Wilson Bulletin. In his annual reports, Charlie regularly thanked Leann for her efforts in keeping the editorial office running smoothly and for catching many of the errors that could plague a publication.

In 1997, Charlie was elected to the Wilson Ornithological Society Council and in 1999 he was elected Second Vice-President of the Society. He succeeded to First Vice President in 2001 and to President of the Society in 2003. During the years he served on the Council, Charlie contributed generously of his time. As Editor, he chaired the Edwards' Prize Committee for 10 years, served for several years on the Student Travel Awards Committee, the Student Presentation Awards Committee, the Research Awards Committee, and the Nice Award Committee, continued to referee numerous articles, and regularly contributed to the Van Tyne Library. His involvement in the Society while continuing active research and teaching served as a model for young academics.

Leann quietly also served the society extensively during that time. After serving on the committee evaluating student presentations for several years, she chaired the Student Presentations Award Committee for two years. She later chaired the Student Travel Awards Committee for two years and the Research Awards Committee for two years. One of Leann's most lasting contributions was changing the way that student presentations were evaluated. She prepared the documents that the committee used to evaluate presentations and provided students with feedback about their presentations, so that even the students who didn't receive awards could benefit from the experience.

The Blems have demonstrated that beside a great man is often a great woman, or vice versa. As a team, Leann and Charlie have helped mold the Wilson Ornithological Society. Therefore, it is with heartfelt respect and gratitude that the Wilson Ornithological Society awards the 2011 William and Nancy Klamm Service Award to Charles and Leann Blem.—Sara R. Morris (Chair), Richard C. Banks, Robert C. Beason, Robert L. Curry, E. Dale Kennedy, and Jerome A. Jackson (Klamm Service Award Committee).
WHAT WERE THEY THINKING? IS POPULATION ECOLOGY A SCIENCE? PAPERS, CRITIQUES, REBUTTALS, AND PHILOSOPHY. By Bertram G. Murray Jr. Infinity Publishing, West Conshohocken, Pennsylvania. 2011: 289 pages, many figures and tables. ISBN: 10-0-7414-6393-8 (paper), ISBN: 13-978-0-7414-6393-7 (hard cover). $16.95 (paper), $7.85 (ebook).—Where in the evolutionary biology literature is there an equation that allows you to predict the mean clutch or litter size of any bird or mammal? You might be thinking that such an equation does not exist or that its formulation is impossible because the biological world is too complex. You would be wrong on both counts. Such an equation does exist and even more remarkable is that it works. Why then is this equation not known to ornithologists world-wide? That, caro letore, is partly the subject of this book. The man who created the equation, the late Bert Murray, was for most of his career almost entirely ignored by ornithologists, ecologists, and evolutionary theoreticians.

By consistently approaching ecological and evolutionary problems in a manner orthogonal to his contemporaries, Murray struggled to get his unconventional ideas published in the scientific literature. Frustrated by the peremptory rejection of his manuscripts, despite detailed, often point-by-point rebuttals of the (usually) anonymous reviewers’ criticisms, Murray shortly before his death began collating some of his rejected manuscripts together as a book. The current volume is the result. The caveat to neutral readers is that these papers failed to get through the scientific review filter; by conventional wisdom they have failed to qualify as scientific literature. However, the unbiased reader who completes the book may join Murray in wondering—as he does in his title—"what were they (the ecologists, evolutionary theoreticians, and referees) thinking"?

Why are the included manuscripts so controversial? To answer this, the reader should understand several things. First, Murray’s guiding principle was the importance of demography and especially the manipulation of life (history) tables in answering questions in theoretical biology (Chapter 3 onwards). While demographic variables (such as age of first breeding) are a core part of life history theory, the presentation and deductions from actual life (history) tables in ornithology or evolutionary biology are astonishingly sparse (e.g., in Charlesworth’s [1994] canonical text there are at most 3 life tables!). Second, Murray’s theoretical insights were centered on two equations: the fundamental (Euler)-Lotka Equation and Murray-Nolan Clutch-size Equation (alluded to in the opening paragraph). The Lotka Equation calculates the intrinsic growth rate (r) of a population and, consequently, has the desirable property that the success (growth) of competing subtypes (be they populations, genotypes, phenotypes or whatever) may be compared. The clutch-size equation Murray originated in 1989 with Val Nolan; it is unique in ornithology in being the only equation to predict the exact clutch-size of a population. Both equations appear frequently in Murray’s book. Third, Murray came to insist that the Kimuran-style Malthusian Parameter is the only correct measure of evolutionary fitness and other fitness measures, like net reproductive rate \( R_0 \) are misleading. He demonstrated this latter theoretical result in 1997, but his paper was characteristically disregarded. An added twist was that at genetic fixation the Malthusian parameter is zero—a profound conclusion because one could metaphorically say that evolution is hunting for genotypes which attain persistence \((r \sim 0)\) in the long-term.

Because Murray’s book is composed of a miscellaneous assemblage of rejected manuscripts, the various papers do not flow sequentially, occasionally repeat the same points, and are disfigured by a number of typos. Unfortunately, the book also ends abruptly at Chapter 8, without any summarizing chapter to synthesize what has been covered in the previous pages—these deficiencies which will make it even more challenging to grasp Murray’s unconventional approach. Ornithologists will find Chapters 3-6 especially relevant. Chapters 1 and 7 are devoted to a discussion of Popperian philosophy and, while I agree with everything Murray writes, many ornithologists will find the content of little direct relevance to their research. Chapter 2 is a
returnation of density-dependent regulation and the Logistic Equation; in its place Murray forwards a new equation to account for a population fluctuating around a long-term mean population size. While highly valuable for ecological theory, it is ornithologically perhaps less so, and I will not discuss this important chapter further. Chapter 8 is a discussion on whether to use the terms ‘mass’ or ‘weight’; Murray makes some insightful remarks, but this is a light-weight contribution (relative to the other chapters) and could have been omitted.

Returning to those chapters more germane to ornithology, Chapter 3 is possibly the most important because it shows how to construct a life (history) table beginning from basics (i.e., a series of population censuses). There are surprises here for those unfamiliar with Murray’s methods, notably the rejection of the standard birth rate equation (and its replacement with an equation of Murray’s own devising) and the use of the fundamental Lotka Equation for populations without a stable age structure. Both these standpoints will be controversial. For the skeptical, working through the numbers will show whether Murray is correct or not. Aside from these points, this chapter contains important considerations relating to avian mating systems. By realizing that the average clutch size must be the same for both sexes but that demographic variables may differ between the sexes, Murray extended the Murray-Nolan Clutch-size Equation to incorporate these inter-sexual demographic differences with what he called the Life History Equation (Chapter 3, page 88 et seq.). This is a significant equation. For the many ornithologists curious why, for example, prairie-chickens (Tympanuchus spp.) are lek-mating polygynists or phalaropes (Phalaropus spp.) are sex-role-reversed polyandrists, Murray’s Life History Equation is a brilliant (if unconventional) assault on these fundamental problems. This is a strong claim, but before consulting the book I ask you to imagine the following circumstances: visualize a population of birds where the males have worse survival than females; imagine, too, that females have an earlier average age of first breeding; also consider that the empirical data show that males have a higher average annual reproductive success than females; finally imagine the primary sex ratio is at unity. Can you deduce what consequences these differing demographic parameters would have on this population, or better derive a single equation which unifies these demographic para-

Chapter 4 is an investigation of the demographic characteristics of a small persisting population of Ivory-billed Woodpeckers (Campephilus principalis), assuming the Big Woods, Arkansas sightings had any validity, and an exploration of the dynamics of small, persisting populations. Because little is known about the woodpecker’s demography, much is inferred in this chapter. Due to these uncertainties, the demographic deductions concerning the Ivory-billed Woodpecker appear less convincing than in other chapters. Nonetheless, there is much of substance here, especially Murray’s Population Equation. The value of Murray’s Population Equation is that if you know the number of eggs laid in a population and have good data on demographic attributes (particularly age-specific survival), then you can easily calculate the number of adults of breeding age as well as the total population. The versatility of this equation allows us to see, for example, that if a long-lived and short-lived population produce the same number of eggs (n_e), the long-lived population attains a greater population size (this is intuitively obvious). However, more enigmatic is the discovery that while the population sizes are quite different, the numbers of breeding adults are almost identical. Other useful insights are contained in this chapter.

Chapter 5 is on Clutch Size and Length of Breeding Season, and shows that clutch size varies inversely with the length of the breeding season, a deduction from the Murray-Nolan Clutch-size Equation. Generally-speaking this relationship must hold, but as Murray observed (page 160) “I t is strange to read the reviewers’ negative but baseless comments (pages 169–183) on this admirable chapter; Murray’s exasperation at this sort of treatment was understandable. Chapter 6 is another extremely important chapter showing the Mayfield Method for calculating nesting success
is flawed. Murray identified three serious problems with the Mayfield Method. Particularly damning is his recognition that daily mortality rate cannot be the number of nest failures divided by the number of exposure days. Remarkably, this manuscript was rejected by approximately six journals (page 186). Murray's lengthy, incisive response (pages 203-236) to the inept Condor reviewers is a tour de force. Those ornithologists still using the Mayfield Method would be strongly advised to read this chapter.

Space constraints preclude discussion of the many other noteworthy insights in Murray's volume. I am satisfied Murray's ideas warrant serious consideration and that rejection of these manuscripts was unjustified. Watching events from Africa, I have been puzzled at the disdainful treatment Murray has received. For instance, in all leading review papers discussing clutch size evolution (e.g., Godfray et al. 1991; Martin 1996, 2004; Ricklefs 2000) there is not a single mention of the Murray-Nolan Equation. Those authors were perfectly entitled to disagree with Murray's theoretical perspectives, but it is unscientific (if not disingenuous) that these authors (and many others) ignore the equation without at least saying something like "we disagree with this equation because of reasons x, y and z". This is even stranger when one remembers the success the equation had in predicting the clutch size of those species to which it was applied. I'm sure Murray's current iconoclastic book will likewise be ignored. The fact Murray focused on populations rather than individuals (which seems [incorrectly] to imply group selection), that he used hypothetical numbers rather than empirical data (ornithologists are a tribe of empiricists), that he avoided sophisticated mathematics and statistics (which often gives a deceptive patina of authority to many texts), and that he unashamedly identified several canonical ideas (like the Mayfield Method) as flawed will simply be too radical for many ornithologists to accept or even entertain—their theoretical arteries hardened years ago. But for those who remain open-minded, Bert Murray's book presents novel theoretical perspectives. These perspectives, in my opinion, come closer to the ultimate resolution of many fundamental evolutionary and ecological problems than any ornithologist has achieved in the entire history of our discipline. I am left to wonder what further evolutionary and ecological insights could be found in the other unpublished manuscripts of Bert Murray that were never accepted for publication.—GREGORY B. P. DAVIES. Curator of Birds. Ditsong National Museum of Natural History (formerly Transvaal Museum), P.O. Box 413, Pretoria, South Africa; e-mail: greg@ditsong.org.za

LITERATURE CITED


HANDBOOK OF THE BIRDS OF THE WORLD. VOLUME 15; WEAVERS TO NEW WORLD WARBLERS. Edited by Josep del Hoyo, Andrew Elliott, and David Christie. Lynx Editions, Barcelona, Spain, 2010: 880 pages, 61 color plates, and 495 photographs. ISBN: 978-84-96553-68-2. $299.15 (cloth).—This volume of the ambitious HBW series with 606 species accounts covers another precise 1/16 of the world's bird species but, given the abundance of weavers and finches, probably much more than this fraction of the world's wild bird individuals. In fact, if the handbooks weighted their treatment of species according to the number of individuals (recent estimates of the world's total ranging from 200 to 400 billion), hundreds of pages would be devoted to the Red-billed Quelea (Quelea quelea) alone, whose estimated population size is in the billions. But hardly a note would then be spared for one of the world’s most spectacular but sadly decimated bird families, the Hawaiian honeycreepers (Drepanididae). Thankfully, Volume 15 gives them ample space, abutting the expansive treatment of their parent family, the nearly globally successful finches (Fringillidae, native everywhere but Australia). Also often called 'finches' but a separate granivorous radiation rooted in Africa is a trio...
of families that fill another large portion of the volume: the weavers (Ploceidae), and their allies the estrildids (waxbills) and viduids (indigobirds and whydahs). Finally, this volume treats the New World birders’ darlings, the wood warblers (Parulidae), often loudly dressed and tastefully voiced, along with their frequent neighbors the vireos (Vireonidae, often loudly voiced and tastefully dressed). The lone Olive Warbler (Pseudramus tenuatus) is probably related to the accentors covered back in Volume 10, but is kept in this volume as its own family next to the warblers for appearance’ sake (i.e., it looks and acts like one) and at least a couple of other putative warblers are stuck here that are probably tanagers. Thus, eight families are covered, including some of the most familiar and well studied birds in the world.

Before diving into the families, following an excellent HBW tradition, the volume begins with an extensive topical Foreword, this one an update to the global state of bird conservation. The 2002 World Summit on Sustainable Development set 2010 as a target deadline to ‘significantly reduce biodiversity loss’. The central message from the four authors, all major players in BirdLife International, is that with respect to birds, we failed. We know a lot more now, but knowledge was never really the main issue. We’ve known enough for a while, but we failed to do much about it. Roughly half of the world’s bird species have declining populations, and one in eight is threatened with global extinction. The most significant threats are agriculture, wood harvesting, and invasive species. The argument, and more generally the presented picture of the current state of bird conservation, is tremendously informative with 58 color figures attractively complementing the textual description of the status of the world’s birds, underlying reasons for the trends, and possible solutions and mitigations.

Typically for the series, the species accounts are preceded by a scholarly but accessible description of the family, with standardized sections: Systematics, Morphological Aspects, Habitat, General Habits, Voice, Food and Feeding, Breeding, Movements, Relationship with Man, Status and Conservation. Interspersed with a generally comprehensive view of the taxonomy, lifestyle, and natural history of the family are samplings from recent and classic behavioral or ecological studies, observations by naturalists, and even literary and historical points relating to the birds or the names we give them. Each author is generally a major scholar—indeed, often the undisputed heavyweight champion—of the respective family. The photographs that accompany these descriptions are stunning, without qualification. A small army of ornithopaparazzi have caught birds in the midst of virtually every aspect of their daily activity—nestbuilding, foraging, courting, copulating, bathing, tending young—and have presented these scenes to us with perfect vibrancy and artistry. Equally exquisite are the wonderfully large plates opposite the accounts, depicting every bird species, including both males and females if dimorphic, and subspecies if they look different.

To criticize an installment of an unprecedented overview of the world’s birds feels somewhat like an exercise in ingratitude, since the very existence of this series—the fact that these people have bothered to do it, and have in the end produced this masterpiece—is inspiring and encouraging. Nevertheless, any critic will always have done it differently. I would have liked to see introduced ranges mapped (the House Finch [Carpodacus mexicanus] is the only species for which this is done, insofar as its introduced range is in the same continent). The absence of citations in the text of the family descriptions renders them much less useful as a scientific resource, because the trouble of searching out the sources of claims is prohibitive. For instance, if we want to follow up on the idea that the head coloration of the Red-headed Quelea (Quelea erythrops) is an arbitrary signal and not an indicator, or that the white tail patches of the Slate-throated Whitestart (Myioborus miniatus) function in startling prey into flight, there is no easy way this can be done. The large General Bibliography (actually a list of authors and dates) at the end of each family description is of very little specific use. But perhaps this and other criticisms I have in mind have a common thread, and reveal that I might not be quite in step with the purpose or the series. Perhaps I am wanting this Handbook to be more a review of the scientific literature, when in fact its function is mainly to introduce us to all of the birds, what they do, how they live, and where they occur. Each family section is like an extended episode of the BBC Life of Birds followed by a field guide on steroids. It is comprehensive in terms of species, but not in terms of what is known about each species. It is
full of photographs of birds in action, but there are no figures or illustrations of results of detailed scientific investigations of these birds. We find loads of behavior and conservation but very little evolution or physiology. There is discussion of phylogenetic relationships, but no trees and only simple (and misleading) subfamily diagrams. After coming to grips with the specific mission or function of the series, one can see this volume meets this function very well. We should expect to read about the cage bird trade, for instance (given the significant role the estrildids and the Atlantic Canary [Serinus canaria] have had), but not necessarily song learning and its neurobiology basis (despite the significant role the Common Chaffinch [Fringilla coelebs], Zebra Finch [Taeniopygia guttata], and Atlantic Canary have had). There are notable exceptions to this general picture, however, especially in the area of evolution, such as the description of speciation by host switch and mimicry in indigobirds, and the excellent coverage of the problems faced when constructing phylogenies of the vireos and finches.

To say that this is a bird lover’s book is not to denigrate it, and even for ornithologists it is much more than a ‘curl up and read shop’ book. There is a wealth of information here suitable for teaching, data mining, example-searching for review papers, and even hypothesis generation. And let’s face it, most of the people who will buy this $300 tome are actually professional ornithologists or at least die-hard birders who know as much as professional ornithologists. Besides, we already know how to search for our references when we need them. That’s boring stuff compared to the delights of this book and of the HBW in general. I look forward to the one last volume to come.—DAVID C. LAHTI, Assistant Professor, Queens College, City University of New York, 65-30 Kissena Boulevard, Flushing, NY 10541, USA; e-mail: david.lahti@qc.cuny.edu
landscapes in many regions may be due to edge effects of desiccation, wind and fire, generalist birds that outcompete forest birds, and increased predation. Linear forest at least 400 m in width may have a short-term chance of conserving some forest species. Many tropical birds of the forest understory in release experiments were reluctant or incapable of crossing a water gap as wide as 100 m. Dispersal experiments and comparisons of bird species in nearby forest patches show continuous areas of forest may be necessary to allow dispersal and immigration of birds between one site and another.

Tropical birds facilitate ecosystem functions through their mobility and spatial link within forests and other habitats as they carry genetic material between plants or habitats (fruit and seed dispersal, pollination), nutrients (resource links include nutrient deposition from sea to land, and scavengers cleaning carcasses and reducing potential diseases), engineer their physical environment (woodpeckers making nesting holes), or control insects. A few birds are specialists that have closely coevolved with their food plants (as in mistletoe-feeding birds that disperse the seeds), but many seed dispersers are not so specialized, but are necessary dispersal agents for plants. Large frugivores have disappeared from many islands and forest fragments, and their dispersal and the regeneration and restoration of forests is limited by the availability of these seed-dispersing birds to find plants with large seeds. Over a quarter of all frugivore bird species are threatened, near-threatened or extinct. Pollination of certain plant species in the Neotropics is largely effected by hummingbirds, and the chapter on ecological functions reviews the foraging behavior of hummingbirds in relation to their body size, bill size and shape, and habitat.

An estimated 42% of bird species have been used by humans. Most wild birds (90% of total) that are caught and survive the international bird trade end up in the European Union; many others go to East and Southeast Asia. The capture and export of parrots in New World is a prime danger to populations; half a million parrots a year are taken from the wild. The wild bird trade also involves the local use of birds, as in Java and Bali where ~36% of households have pet birds with most of these caught within Indonesia or bred in captivity. Local use of birds may have decimating effects, as in over-harvesting of eggs of an endangered Indonesian megapode, the Maleo (Macrocephalon maleo). Commercial exploitation in Indonesia of nests of swiftlets Collocalia spp. for bird-nest soup is intense. The eggs of Edible-nest Swiftlet (Aerodramus fuciphaga) are sometimes taken from their nests and cross-fostered in the nests of colonies of Uniform Swiftlet (A. vinikorensis). The edible nests are then exported to China, but this cross-fostering in swiftlet farming in attempts to sustain the population may result in inter-species hybridization. Sustainable harvests of birds with take rates ascertained from demographic models may allow local subsistence and recreational hunting, as for Magpie Goose (Anseranas semipalmata) in northern Australia. A few species are threatened with extinction due to human use (e.g., African vultures which are killed for traditional medicine), but the threat is nothing like that due to loss of their habitats.

Conservation concerns for migratory birds that winter in the tropics have focused on preserving their abundance. The decline of migratory songbird populations in the temperate region may in part be due to a decrease in suitable wintering habitats, but the evidence is sparse. The migratory connectedness of breeding and wintering populations across a wide geographic scale is being studied with new technologies of stable isotopes (plumages grown in the wintering region may have stable isotope ratios that are characteristic of the wintering sites), by molecular genetics for maps of populations in breeding areas and the tropics, and by radiotelemetry. Not considered in the migration chapter are other sources of information on connectedness, such as: (1) subspecific identification of birds in their summer- and winter-use areas, and (2) banding recoveries. Some connectivity of migratory songbirds is known, for example in Indigo Buntings (Passerina cyanea) (R. B. Payne. 2006. Birds of North America. Number 4), where banding recoveries show the birds maintain their east-west spatial distribution in the New World between breeding areas, stopover sites in migration, and wintering areas. The recovery data in the U.S. Geological Survey, Bird Banding Laboratory, should be examined for geographic connectedness of summer- and winter-use areas of other migratory birds, as these data are certain and precise, and the recoveries can inform conservation strategies.

The term ‘bleak’ characterizes the long-term prospect for birds in the tropics. Considering the
Time lag for populations to be lost after degradation of their habitats, forest areas as large as 10,000 ha may lose many bird species within 100 years. The chapter on climate change describes the future of tropical birds as nothing if not a disaster. Their sedentary behavior and the large spatial scale of their forest habitats indicate that most birds will be unable to shift sufficiently fast or far to keep up with rising temperatures when these affect their habitats over the next few decades. Climate change also affects birds by increases in diseases, such as bird malaria, and by increasing seasonality and variability of rainfall, and in land and sea temperatures.

Errors are few; the only howler I noted was the reference (page 82) of tropical forest species with small clutch sizes, lower productivity, and longer life spans as 'r-selected' life histories (rather than 'k-selected'). The term, 'r-selection' in the 1970s and 1980s, following MacArthur and Wilson's work on island biogeography, was used to describe species with a life history of rapid reproduction, and 'k-selection' to describe species with traits that promote competitive success and survival. The terms came from growth curve equations, where 'r' was an exponential factor in population growth and 'k' was the carrying capacity of the environment. The book index includes both bird species and localities. The maps, graphs and photographs are more visually compelling in the color plates than in the corresponding black and white images in the chapter texts.

The book is a useful reference on the conservation ecology of tropical birds. As many as 600 threatened bird species do not have a single published study on their biology, and there is much to be done in this field; the results may inform conservation strategies. I recommend the book to anyone with an interest in bird ecology and conservation and in birds of the tropics.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48104, USA; e-mail: rbpayne@umich.edu

The Birds of Panama: A Field Guide. By George R. Angehr and Robert Dean. Zona Tropical/Cornell University Press, Ithaca, New York, USA. 2010: 456 pages. ISBN: 978-0-8014-7674-7. $35.00 (paperback).—On a natural fence-row at the edge of a pasture, flitted a small yellow bird with an orange tint to its face. A quick thumbing to the flycatcher section of Angehr and Dean's new field guide confirmed my suspected identification, Ochruc-lored Flatbill ("Yellow-breasted Flycatcher" in Angehr and Dean, Tolmomyias flaviventris), a recent colonist from northern South America into eastern Panama. The illustration of this species on page 234 is spot on whereas it is unmentioned, let alone illustrated, in Ridgely and Gwynne's 1989 second edition of A Guide to the Birds of Panama (Princeton University Press). This trip to the Darien Province of eastern Panama was my first with Angehr and Dean's new field guide, and I've been using it almost exclusively ever since.

Replacing an icon is always difficult but, in the more than 20 years since Ridgely and Gwynne, much has changed both in the printing world and in Panama. Perhaps most importantly, the cost of color printing has decreased substantially, and an entire glossy book with plates on the right side of every page-pair is economically feasible. Thus, Angehr and Dean is a 'second generation' field guide in the spirit of the iconic National Geographic Field Guide to the Birds of North America, sharing the conventions of the dominance of graphics over text, full-body paintings of all bird species regularly found in the region, and color-coded range maps—all in a format emphasizing portability over an exhaustive review of natural history. The result, in the case of Angehr and Dean, is one of the best examples to date of the contemporary Neotropic bird guide. Let's be clear: the zealot may wish to keep a copy of Ridgely and Gwynne in the car, hotel, or home office, but this new guide is the one book that the bird enthusiast in Panama will want to carry in the field, and also makes for the best go-to office reference for questions of currently-known distribution. This book also benefits from over two decades of additional field expeditions, both by museum ornithologists and avocational bird enthusiasts. Areas such as the Rio Changuinola, Burica Peninsula, Coiba Island, Cerros Hoja and Chucanti, and the Piñas-Jaque region are among a myriad of localities that had only been visited by one or two collecting parties at the time Ridgely and Gwynne was drafted. It is no exaggeration to say that Angehr and Dean's Panama is a quite different ornithological landscape compared to just 20 years ago.

George Angehr is the leading authority alive on the birds of Panama. Over the last decade, Angehr
has developed a reputation as a stickler for the details about Panamanian bird distributions, and this book represents the fruits of his attention to detail. Robert Dean is a gifted bird artist who balances attention to species-specific differences between closely-related taxa while depicting birds as vibrant and life-like, without resorting to the harque. Not only do Dean’s birds have depth, they are usually posed correctly for the species, which can be a significant aid in proper identification (but I am not sure I have ever seen a female Great Antshrike [Tarakba major] on the ground, page 203). The critical part in each of Angehr’s species descriptions is the text in bold, which points out key phenotypic characters or geographical restrictions for a given species. The text might stray a half dozen or so words beyond the minimum for some species, but I doubt many readers will quibble.

The range maps really drive home the biogeographic complexities of diminutive Panama, and it is easy to overlook the considerable amount of information they convey. The maps use three colors: purple for residents, blue for boreal migrants, and red for auroral migrants with crosshatching used to convey a pattern of erratic visitation rather than year after year site fidelity of non-breeding visitors. This scheme just works and the new user quickly assimilates this scheme without having to refer to a key or guide. It is important to note the range maps are scaled, depending on how widely distributed the species is in Panama. Care was taken to make sure the reader does not get disoriented when zoomed into a small region in Panama.

One caution for the reader is that many of the range maps likely overstate the continuity of many species ranges between the extremes of their distribution. The most egregious example is the Orange-billed Sparrow (Arrenonom aurantirostris), which has been found in isolated patches of humid woodland habitats along the Pacific lowlands of Panama, but cannot be found in most of this arid and savanna-like region despite the range map on page 360. Even some published distributional gaps, such as that of the Bay Wren (Contorchilus [Thryothorus] nigricapillus) east of Panama City (Gonzalez et al. 2003, Condor), are missing from Angehr and Dean’s range maps. These details are unlikely to affect most users in the field, but could be corrected to meet the standards of excellence displayed elsewhere in the book.

Dean previously illustrated Zona Tropical/Cornell University’s The Birds of Costa Rica: a Guide (Garrigues and Dean 2007), and many of the illustrations in the Panama guide are borrowed from that earlier effort. However, perhaps as many as a third of the widespread landbirds in Panama show racial variation between eastern and western Panama. The majority of these represent subtle differences in plumage coloration and size that would be difficult to appreciate in the field and irrelevant for a compact field guide. Perhaps one in five of these cases represents discrete differences in plumage that might confuse the traveling bird enthusiast. Dean and Angehr illustrate both eastern and western forms for several of these, such as the Bay Wren or the White-shouldered Tanager (Tachyphonus lectugii). However, often only the western form is illustrated, and the form occurring in central and eastern Panama is not. A small caption next to the illustration, in many of these cases, notes that it is the western form that is illustrated, along with a verbal description of the eastern form in the text.

Nonetheless, there are too many instances where no illustration exists for a variant likely deserving species-level status (the Blue-crowned Motmot complex, Momotus [momota] coeruliceps), for the form most likely to be observed in Panama (e.g., Ruddy Foliage-gleaner, Automolus rubiginosus), or both (e.g., Ochre-bellied Flycatcher, Mionectes oleaginosus).

One final frustration with the layout is a tendency for phenotypically similar birds to be spread across multiple pages. For example, flycatchers with kiskadee-like plumages are spread across three pages in the book, while resident Catharus thrushes are split across two pages. Possibly I just cannot let go of the ‘Field Guide 1.0’ mentality, but I appreciate these birds all on the same page so that my eye can quickly pick out the discriminating field marks without having to leaf back and forth. Ironically, this isn’t as much of a problem in the similar, but sveter, Zona Tropical Costa Rica guide. The problem is not a lack of space on the figure pages; some figure pages have so much white space that the birds appear to be floating in mid air. Instead, the problem seems to be due to excessive white space on the text page. The Panama guide has what appears to be 1.5-line spacing between species accounts whereas the Costa Rica guide uses a solid line rather than excessive white space between species descriptions and has considerably less white space.
at the header and footer. To be fair, this is really only a problem for species-rich groups, namely hummingbirds and flycatchers; for nearly all other families, users won’t be subject to excessive page-flipping.

We have yet to see in the Neotropics what I consider a third generation field guide, exemplified by David Sibley’s *National Audubon Society: The Sibley Guide to Birds* (2000, Alfred A. Knopf). Such a guide would include male, female, and immature plumages of all subspecies and racial variants—perhaps the only effective way to draw attention to the hidden diversity obfuscated by current taxonomy of Neotropic birds. Yet one shudders to think of the size of such a book, even for a small Neotropic country such as Panama. Rumor has it that Angchir, Dean, and Zona Tropical/Cornell University are contemplating a version of the Panama field guide for tablet computers. Leapfrog development, such as skipping over the installation of landlines for cellular phone networks, is common in the developing world. I encourage the authors and publishers to stand firmly on the excellent foundation that is *The Birds of Panama: A Field Guide* and take that leap.—MATTHEW J. MILLER, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092 Panama, Republica de Panama; e-mail: millerma@si.edu

SECOND ATLAS OF THE BREEDING BIRDS OF MARYLAND AND THE DISTRICT OF COLUMBIA. Edited by Walter G. Ellison. The Johns Hopkins University Press, Baltimore, Maryland, USA, 2010: 520 pages. ISBN: 978-0-8018-9576-0. $75.00 (cloth).—Nowhere is the maturation of the modern American birding community more evident than in the current “second wave” of bird atlasing in several U.S. states and counties, as well as in parts of Canada. Even before its first bird atlas effort was complete in 1987 (published in 1996), the Maryland Ornithological Society’s Atlas Committee realized that rapid changes in the status and distribution of many bird species were occurring, and the time to begin a second effort was only a few years away. Planning for this second effort began as soon as the first had concluded, and this atlas work was conducted during 2002-2006.

The late 20th century had seen not just a tremendous boom in real estate development through much of Maryland but also substantive changes in agricultural and land management practices, and in the quality and extent of many natural habitats. The warming climate also appeared to be having an impact on the distribution of several species in the state; others were simply vanishing for reasons unknown. With snapshots of bird distribution just 20 years apart, and with data collected at the “neighborhood level,” associating species’ distributional changes with particular factors becomes more feasible, and the minute detail of both Maryland atlas efforts certainly lends itself to a more precise understanding of bird population dynamics.

Maryland may be ideally suited to lead this second wave of American atlases in the United States. The state is relatively small but, unlike other small states such as West Virginia, and Maryland and the District of Columbia have a surfeit of birders and field ornithologists; these people are devoted both to their state and to its 23 counties, whose avifaunas they know exquisitely well. The Maryland Ornithological Society (MOS) learned a great deal from the earlier atlas work and, for the second, numerous innovations were crucial for planning, execution, and publication. MOS retained a full-time, professional atlas coordinator, Walter G. Ellison, who was also responsible for the production of the publication itself. Ellison worked with both the Atlas Committee and a set of county coordinators, who vetted data from >1,000 volunteers in the field. These volunteers and coordinators were able to submit data from their field cards directly into an on-line data base, an innovation that surely saved many thousands of hours of work, compared to atlas work of the 1980s.

Maryland’s size also permitted volunteers to collect data on an even smaller scale than in other states, the “quarter block,” measuring 2.5 × 2.5 km rather than the standard 5 × 5 km. This finer scale was used in counties experiencing the most drastic changes, whether because of development (Baltimore, Prince George’s, Montgomery, Howard, southern Carroll) or possibly because of changing climate; mountainous Garrett County, in the far western part of the state, and marshy Somerset County, the farthest south.

The Atlas Committee also forged strong ties with agencies at the state and federal levels, which provided both funding and expertise. The Wildlife Heritage Division of the Maryland Department of Natural Resources and the Biological Resources Division of the U.S. Geological Survey at
Patuxent Wildlife Research Center partnered with MOS with the express intent of making this second atlas 'a model for establishing a nationwide network to monitor changes in bird population,' as Ellison notes. Data management for the second atlas 'a model for establishing a nationwide network' was conducted in coordination with the National Biological Information Infrastructure and with an eye to the most advanced practices from recent European atlas work. This remarkable alignment of agencies and resources was further helped by the generosity of many thousands of landowners, who welcomed atlasers onto their properties, and by considerable financial contributions from private individuals from all over the region, many of whom also volunteered their time as atlasers.

All 1,284 atlas blocks were covered at least once, and most were covered multiple times, with >190,000 bird records entered in the main data base. Highly qualified volunteers also conducted 'mini-routes,' as in the first atlas project, to provide an index of species abundance, not just distribution. This method involves making 15 3-min stops at fixed points, and all species detected are recorded for each stop. Data from these mini-routes were maintained in a separate data base and compared to earlier results.

Two species were recorded breeding for the first time ever in Maryland during the second atlas work, Common Merganser (Mergus merganser) and Ruddy Duck (Oxyura jamaicensis). Three species, Northern Shoveler (Anas clypeata), Wilson's Plover (Charadrius wilsonia), and Be-wick's Wren (Thryomanes bewickii), all documented nesting during the first atlas, were not detected during 2002–2006. In all, 206 species were found nesting in Maryland and the District during the second atlas, and accounts for these species occupy the bulk (404 pages) of the present volume. The editor and many volunteer authors of these accounts, in lucid, terse prose, offer not just a comparison of past and present status but also an overview of environmental and other factors that have led to changes in distribution or to decreases and increases in populations, as well as providing copious specifics on the discovery and documentation of exceptional records.

As in the first atlas, each species account occupies just two pages: the first page has text and a photograph of the species, and the facing page has up to five maps and charts. The latter page typically includes: a map depicting the number of atlas blocks in which the species was detected (and at what category of certainty for nesting activity); a map depicting the difference in bird distribution/detection between the first and second atlases; a map depicting the species' relative abundance (from the mini-routes); a chart showing the change in total blocks between the two atlases (by region); and a graph illustrating the results of the Breeding Bird Survey from 1966 through 2006.

These species accounts are compact, but one may spend nearly an hour poring over just a single one, as they are data-rich and thought-provoking. The accounts may not hold many surprises to veteran students of bird distribution in the mid-Atlantic; the dynamics of so many of the species that are losing or gaining ground are familiar from adjacent states as well. However, to see these changes depicted at small scale, by a project whose protocols were clearly professional, is breathtaking, especially for species such as Northern Bobwhite (Colinus virginianus), which has essentially disappeared from most of Maryland in the span of two decades, from the foothills of the Alleghenies to Cecil County in the northeastern part of the state. Just a glance at maps for Grasshopper Sparrow (Ammodramus savannarum), Common Nighthawk (Chordeiles minor), and Eastern Meadowlark (Sturnella magna) tells a similar story about the costs of urbanization, and maps for Prairie Warbler (Dendroica discolor), Yellow-breasted Chat (Icteria virens), Yellow Warbler (Dendroica petechia), Eastern Whip-poor-will (Caprimulgus vociferus), Black-and-white Warbler (Mniotilta varia), and Kentucky Warbler (Oporornis formosus) show that many birds of successional and forest edge habitats no longer nest across large areas of the state where they were widespread just a few years ago. For anyone who works in bird conservation at the regional level, these species accounts (and related data), along with Breeding Bird Survey data, provide the best information available for the prioritizing of land acquisition, preservation, and management on behalf of nesting birds.

One of the greatest improvements from the first atlas, in terms of presentation, is the use of color printing for the second atlas, which makes interpretation of maps far easier. The second atlas does not reproduce all of the front and back matter of the first (which had more extensive sections on physiography and climate, for instance) but presents photographs of habitat types and land-
use maps, both very useful for understanding the text and maps within the species accounts. It was a pleasure to see drawings of birds, many by the state's birders, in the first atlas, and we now enjoy seeing photographs by many of the state's most active birders in the second. This volume is a credit to the large team responsible for it and in particular to its watchful editor, Walter Ellison. The raw data are available in electronic form from the MOS for researchers wanting to draw on still more detail than the book offers.

The only unfulfilled desideratum in the atlas is perhaps unreasonable: the reader would relish information on the avifauna of much earlier periods and also on the additional 230 or so bird species documented in Maryland and the District of Columbia but not known to breed there. A few recent volumes (such as San Diego County Bird Atlas of 2004) have included such material, allowing readers to consult a single reference for status and distribution of all bird species. We are assured that Maryland birders have already embarked on a massive electronic data base that will include essentially all reliable bird records that have associated geographic data. If the teamwork and urbanity evident in their atlases are any indication, we anticipate outstandingly polished and rich results.—EDWARD S. BRINKLEY,
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SHOREBIRDS OF NORTH AMERICA, EUROPE, AND ASIA, A PHOTOGRAPHIC GUIDE. By Richard Chandler. Princeton University Press, Princeton, New Jersey, USA. 2009: 448 pages, 850+ color photographs, and 134 color maps. ISBN: 13-978-0-691-14281-4. $35.00 (paper).—There is perhaps no other group of birds that has had so many books published that consider identification as the shorebirds. This is certainly no surprise as they can be difficult to identify in some cases, but in other situations they are vibrant and colorful. They are interestingly complex with regards to field separation, but yet attractive and charismatic. One of the classic volumes on this group was Richard Chandler's North Atlantic Shorebirds published in 1989. It was one of the first books to attempt to simplify the identification of this group of birds through use of high quality photographs in particular using standardized poses that were as comparable and easy to use as field guide paintings. Furthermore it included many amazing photographs of shorebirds in flight, a rarity in that day. Many books have come since then, including some with rather innovative and varied use of imagery. Some of these have attempted to achieve a feel for the shape and form, as well as how shorebirds look in the context of habitat, not simply comparative in terms of plumage. Thus, it was with great interest that I received Chandler's new book Shorebirds of North America, Europe, and Asia: a photographic guide (Shorebirds henceforth) to review. The field of photographic guides to shorebirds is more crowded now, and certainly a question is if this new book fills a need or niche for researchers and shorebird observers.

In the introduction Chandler notes this book grew out of his original North Atlantic Shorebirds and the similarities in structure are clear. Chandler also indicates his goal is to illustrate, photographically, identification and age criteria, focusing on features that are usable in the field with in-hand features not considered for the most part. It is interesting to compare the new volume with its progenitor as it clarifies how much has changed in the intervening years, including how much more we know about identifying these birds, but also that the quality of visual material today is so much better than even the classics such as Chandler's earlier book. For example, today photographic reproduction is of higher quality, and less expensive color reproduction allows for a much more visually stunning volume using over 850 photographs. Shorebirds includes most of the species in the northern hemisphere as described in loose zoogeographical terms rather than all the area north of the equator. This definition allows for inclusion of 134 species; however, if their range extends to regions outside the northern hemisphere, it is also mapped, which is quite helpful.

The book's introduction of 30 pages is nicely illustrated. It includes some standard sections such as the topography of a shorebird, explanation on how to use the maps, and accounts as well as two major subsections. These are Plumages and Molts, and Shorebird Behavior. The latter describes primarily various aspects of foraging, and is lavishly illustrated. What is missing here is any information on territorial or sexual displays by shorebirds, and this may be because these are seldom seen where most observers live or observe. Reproductive displays are of such complexity and interest that they deserve at least
some mention in the introduction. Furthermore, some shorebirds are rather similar in appearance, such as the North American dowitches (Limnodromus scolopaceus and griseus) to give one example, yet the displays are quite different in these closely related species. Another point to be made is that foraging is dealt with well, but habitat, and not only foraging habitat but breeding habitat, is given almost no space. These birds travel half way around the world to get to specific breeding areas; some summary of what makes these breeding habitats special would have been good to include. Finally, migration itself is not detailed. These are among the most impressive avian migrants that exist! While some long-distance journeys are noted in the species accounts, some information in the introduction regarding migration and vagrancy would have been good.

The other subsection in the Introduction is that of Plumages and Molts, and it is nicely detailed, complete and well illustrated. The images of juvenile plumage patterns are very helpful. However, the molt terminology used is not the standard Humphrey-Parkes system that North American ornithologists and also many bird identification enthusiasts have come to expect. There is a chart that notes 'equivalents' of various plumage naming systems, although this is only somewhat useful as the Humphrey-Parkes (H-P) system is not always equivalent to other systems, and in these particular differences it's where H-P becomes most useful. It will be a disappointment to many North Americans that the H-P molt naming system was not used, particularly as it allows for a more precise comparison of plumages between species. It also appears that in cases where molt differences are very helpful in separating similar species, such as the American and Pacific Golden plovers (Pluvialis dominica and fulva, respectively), this molt information is not included in the main identification summary. Instead, it is relegated to a later section and then, at least with the plovers, only treats differences in timing of body plumage rather than the more important differences in timing of wing molt. These differences in timing of the wing molt, by age, and the corresponding differences in wear later in the year are not noted at all. These may be nitpicks, but shorebird identification knowledge is rather detailed these days, and the quality of high-powered optics and ability to take precise photographs of these features allows for use of very nitpicky features to aid in identification. Given that the imagery in this book is so fantastic, I note the few instances where the text does not come up to par with the fabulous imagery.

The main body of this book is of course the species accounts. The 134 species are well illustrated, and this includes an undescribed plover ("White-faced Plover" [Charadrius sp.] from South Asia), as well as some extremely rare species such as the Slender-billed Curlew (Numenius tenuirostris). The Eskimo Curlew (N. borealis) is not illustrated. Each account is divided into various sections: Identification; Plumages by Age and Time of Year; Calls; Status, Habitat and Distribution; Racial Variation; Similar Species; and References. Each species account is accompanied by a range map and various images of the species in different life stages, and usually in flight. It is a shame that the map didn't include migratory routes, although the maps themselves are of sufficient size to see details and are color coded seasonally and easy to read.

The real reason you want to have this book is the fantastic set of images included. The images appear to be very carefully chosen to illustrate each age or plumage well, they are almost all side-on images and standardized in pose so that they all point to the right and the bird in the image is approximately the same size within species or related species. Chandler, for the most part, uses classical 'portrait' style photographs, in other words up close, and in detail. Shorebirds in its layout and style of photography used makes comparisons between species easier and more direct. Similarly, Chandler's book makes it straightforward to review differences in age classes and plumages within species. The images in Chandler are truly stunning, and very, very useful. I find that, when wanting to know what a bird actually looks like, I go to this book first; when I want to study fine feather details, and characteristics that are particularly along the 'nitpicky' end of the shorebird identification continuum, I turn to this book.

Given that there have been some important contributions to the shorebird identification field in the last few years, it is necessary to compare this book to them in some manner. Perhaps the most innovative book in recent years dealing with shorebirds is The Shorebird Guide (M. O'Brien, R. Crossley, and K. Karlson. 2006. The Shorebird Guide. Houghton Mifflin Co., Boston, Massachusetts, USA). That book makes the argument that
showing the birds in distant views, in odd angles, in direct comparison to other species, hidden in flocks for example creates a realistic situation that can be used in the field to much more easily identify the birds. In a sense, this trains for better identification as it duplicates in the book some of the complexities of field observation. I agree to a great extent, but I also see the other side. The other side is that to obtain that initial grounding on what shorebirds look like, it is useful to have clean, directly comparable, and standardized imagery. It may not be as you see them always in the field, but I find it incredibly useful to go back and forth with images that are setup to show you the differences. In a sense the two methodologies are the ends of two extremes, in a range that you need to master at both ends to become truly proficient in shorebird identification. Chandler’s book stands up well to *The Shorebird Guide*, and if one really wants to know these birds well, having both of these books is imperative.

The reason is that the differences in style and methodology of these two books give different and complementary ways to look at shorebirds and their identification. I readily accept and encourage approach of identifying birds through a more holistic impression approach. In reality, this is one side of a two-sided coin, looking at specific feathers, patterns, and colors complements the impression approach, particularly when first learning to identify the species. Chandler’s book does very well at detailed comparisons, both through the photographs and the text. If you are interested in shorebirds and their identification, you must have this book. We are lucky to be living in an age where photographs and optical equipment are of such quality that they nearly allow for as much detailed study as a museum skin!—ALVARO JARAMILLO, San Francisco Bay Bird Observatory, 524 Valley Way, Milpitas, CA 95035, USA; e-mail: ajaramillo@sfbbo.org
The Ninety-second Annual Meeting of the Wilson Ornithological Society was held in joint session with the Association of Field Ornithologists and the Cooper Ornithological Society from Wednesday, 9 March, through Sunday, 13 March 2011, at the Younes Conference Centre in Kearney, Nebraska. Mary Bomberger Brown, Director of the Tern and Plover Conservation Partnership, University of Nebraska, School of Natural Resources, chaired the Committee on Local Arrangements, which included Chris Thode, also of the Tern and Plover Conservation Partnership; T. J. Fontaine and Karie Decker, University of Nebraska, School of Natural Resources and USGS Nebraska Cooperative Fish and Wildlife Research Unit; Joel Jorgensen, Nebraska Game and Parks Commission; Wayne Mollhoff, Nebraska Ornithologists’ Union; Jacki Loomis, Elaine Connelly, Mark Mesarch, Gregg Hutchison, Sue Ellen Pegg, and Sarah Rehme, University of Nebraska, School of Natural Resources; Paul Johnsgard, University of Nebraska, School of Biological Sciences; Lctitia Reichart, University of Nebraska at Kearney, Department of Biology; and Sarah Focke of the Kearney Visitors’ Bureau. The local sponsors included the Nebraska Ornithologists’ Union; Nebraska Bird Partnership; Nebraska Game and Parks Commission; University of Nebraska, School of Natural Resources; Rainwater Basin Joint Venture; USGS, Nebraska Cooperative Fish and Wildlife Research Unit; Nebraska Birding Trails; and the Kearney Visitors’ Bureau.

The Council met from 0806 to 1654 hrs on Wednesday, 9 March, at the Younes Conference Centre. That evening there was an ice-breaker Social for the conferees and guests, also at the conference center.

The scientific program began on Thursday morning with four concurrent sessions. Each society sponsored its own plenary lecture, scheduled on consecutive days. On Thursday afternoon, the 2011 WOS Margaret Morse Nice Medal recipient, Richard N. Conner, presented the plenary lecture "The ecology of the Red-cockaded Woodpecker, by necessity a multidiscipline study." On Friday afternoon, Gary L. Krapu presented the AFO plenary lecture, "Sandhill Cranes and the Platte River: a local and global perspective," and on Saturday afternoon, Thomas B. Smith presented the COS plenary lecture, "Diversification along ecological gradients in the tropics."

In addition to the plenary lectures, the scientific program included a remarkable 271 presentations organized into 34 sessions, 75 posters, and four symposia on Cerulean Warbler (Dendroica cerulea) breeding biology and migratory behavior, research on North American prairie grouse, avian conservation and ecosystem services in agricultural landscapes, and Piping Plover (Charadrius melodus) and Least Tern (Stern antillarum) management on the Great Plains.

The Local Committee hosted field trips each morning and afternoon to the Rowe Audubon Sanctuary, where attendees could observe from blinds the spectacular assemblage of migratory Sandhill Cranes (Grus canadensis), geese, and ducks at their staging area along the Platte River. Additional field trips before, during, and after the conference included bird watching in the Rainwater Basin of south-central Nebraska; observing Greater Prairie-Chickens (Tympanuchus cupido) and Sharp-tailed Grouse (T. phasianellus) displaying on a lek near Mullen, Nebraska; and visiting the Great Platte River Road Archway, a museum commemorating the westward migration across the Great Plains by covered wagon.

On Saturday evening the conferees gathered for a reception prior to the annual banquet. The evening events included an enjoyable dinner and afterwards AFO President Scott Johnson, on behalf of all three societies, offered our gratitude to the Local Committee for a successful conference. President Johnson then introduced WOS President Dale Kennedy, who thanked the three elected members of Council who had completed their terms of office. Jameson F. Chace, Sara R. Morris, and Margaret A. Voss, and welcomed the three newly elected members of Council, William H. Barnard, Mark E. Hauber, and Margaret I. Hatch. President Kennedy also congratulated the newly elected WOS President Robert C. Beason, whose term would begin at the close of the meeting, and gave to him the WOS ceremonial presidential gavel. The following WOS awards
and commendations also were presented at the banquet, or previously at the WOS Business Meeting:

**MARGARET MORSE NICE MEDAL**
(for the WOS plenary lecture)

Richard N. Conner, “The ecology of the Red-cockaded Woodpecker, by necessity a multidiscipline study.”

**EDWARD’S PRIZE**
(for the best major article in Volume 122 of The Wilson Journal of Ornithology)


**STORRS L. OLSON PRIZE**

Storrs L. Olson, for his review of “The curse of the Labrador Duck. My obsessive quest to the edge of extinction,” by Glen Chilton.

**WILLIAM AND NANCY KLAMM SERVICE AWARD**
(for distinguished service to the Wilson Ornithological Society)

Charles R. and Leann Blem.

**LOUIS AGASSIZ FUERTES AWARDS**

Juan Pablo Gomez, University of Florida, “Turnover of bird communities along a tropical precipitation gradient in Colombia.”

Irene Liu, Duke University, “Relationship between genetic diversity and extra-pair mating in populations of a songbird.”

**GEORGE A. HALL/HAROLD F. MAYFIELD AWARD**

D. Archibald McCallum, of Eugene, Oregon, “The coevolution of repertoire and syntax in Empidonax and allies.”

**PAUL A. STEWART AWARDS**

Carol Brackett, East Carolina University, “Reproductive ecology and population genetics of the King Rail on MacKay Island National Wildlife Refuge, North Carolina.”

Catherine Dale, Queens University, “Variation in cognition and migratory strategy in a partially migratory passerine.”

Ryan Germain, University of British Columbia, “Effects of individual phenotype vs. nest site quality on reproductive success in birds.”

Raphael Lavoie, Queens University, “Effect of migration patterns on mercury exposure in fish-eating birds.”

Dugan Maynard, University of Windsor, “Male quality and female mate choice in a tropical lekking bird, the Long-tailed Manakin.”

Alyssa Stephenson, California State University, Fullerton, “Spatial and temporal foraging patterns of nesting Elegant Terns (Thalasseus elegans) in southern California based on GPS tracking.”

Matt Wilkins, University of Colorado, “A test of the functional role of Barn Swallow trill rate and its implications for song evolution and population divergence.”

Theodore Joseph Zenzal, University of Southern Mississippi, “Habitat and resource use of Ruby-throated Hummingbirds (Archilochus colubris) at a coastal stopover site during fall migration.”

**ALEXANDER WILSON PRIZE**
(for the best student paper)

Nicole M. Davros, University of Illinois at Urbana-Champaign, “An experimental test of density-dependent reproduction in Prothonotary Warblers, Protonotaria citrea.”

**LYNDS JONES PRIZE**
(for the best student poster presentation)

Valerie Steen, USGS Alaska Cooperative Fish and Wildlife Research Unit, “Potential effects of climate change on the distribution of waterfowl and shorebirds in the Prairie Pothole Region, USA.”

**NANCY KLAMM BEST UNDERGRADUATE STUDENT ORAL PAPER AWARD**

John A. Pourtless IV, Florida State University, “An interpretation of the tenth skeletal specimen of Archaeopteryx.”

**NANCY KLAMM BEST UNDERGRADUATE STUDENT POSTER AWARD**


**STUDENT TRAVEL AWARDS**
(presented jointly by AFO, COS, and WOS)

Aubrey Alamshah, Ohio Wesleyan University, “Maintenance behavior trends of the House Sparrow (Passer domesticus).”
ANNUAL REPORT AND REVISED BY-LAWS

Catherine Alsford, Canisius College, "Breeding biology of a newly established population of House Wrens."

Tyler Beck, Florida Atlantic University, "The importance of treatment wetlands as avian habitat in South Florida."

Stefanie Bergh, University of Minnesota, "Detection and occupancy of American Woodcock during singing-ground surveys."

Than Boves, University of Tennessee, "Cerulean Warbler response to anthropogenic disturbance in the Appalachian Mountains: how source-sink dynamics, ecological traps, and landscape-dependent habitat selection impact management and conservation of a declining songbird."

Melissa Creasey, Trent University, "The effects of selection harvesting on Black-throated Blue Warbler reproduction."

Anthony Dalisio, Emporia State University, "Investigation of song dialects in alpine-breeding birds."

Blake Grisham, Texas Tech University, "Understanding the thermal tolerance of nesting Lesser Prairie-Chickens to predict population level influence of climate change."

Matthew Hayes, University of Wisconsin-Madison, "Male and site fidelity of breeding Sandhill Cranes in a dense population in Wisconsin."

Kyle Horton, Canisius College, "Flight calls in wood-warblers: a novel method to study this behavior."

Julie Jedlicka, University of California, Santa Cruz, "Conservation of avian species strengthens ecosystem services in California vineyards."

Erik Johnson, Louisiana State University, "Ectoparasites reduce feather growth in an Amazonian forest bird, Williaemis picoiliolae."

Stephanie Kane, Fort Hays State University, "Effects of multiple habitat management practices on breeding habitat usage by Eastern Black Rail."

Laura Kearns, The Ohio State University, "Influence of prior fate and nest predator community on renesting decisions of multibrooded forest songbirds."

Johanne Kellermann, University of Arizona, "Seeking the endless summer: phenology and plasticity of spring migration in the Southwest."

Janice Kelly, Texas Tech University, "Post-breeding public information use in a ground-nesting songbird community."

Jessica Klassen, Texas A&M University, "Canopy characteristics affecting avian reproductive success: the Golden-checked Warbler."

Meadow Kouffeld, University of Minnesota, "Landscape scale habitat selection by male Ruffed Grouse in northern Minnesota."

Linda Lait, University of Lethbridge, "Post-glacial recolonization of the Chestnut-backed Chickadee (Poecile rufescens)."

Diane Landoll, University of Oklahoma, "Extra-pair paternity and morphological correlates in the Scissor-tailed Flycatcher (Tyranus forficatus) in southwestern Oklahoma."

Teresa Lorenz, University of Idaho, "Spring-summer space use by Clark’s Nutcrackers in Washington State."

Jennifer Ma, SUNY-ESF, "Songbird richness and abundance across a gradient of terrestrial calcium availability in the Adirondack Park, New York."

Monika Maier, Utah State University, "Not just a walk in the park: Clark’s Nutcracker in declining habitat."

Chris McCreedy, University of Arizona, "Drought-delay impacts on productivity for Sonoran Desert breeding birds."

Bailey McKay, University of Minnesota, "The challenge of delimiting recent lineages: the Chinese/Taiwan Bulbul (Pycnonotus sinensis/taiwanus) complex as a case study."

Mduduzi Ndlovu, University of Cape Town, "Phenotypic flexibility of a southern African duck Aythya aegyptiaca during moul: do Northern Hemisphere paradigms apply?"

Jessica Oswald, University of Florida, "Late Pleistocene passerines from the Talara tar seeps in northwest Peru."

Nicholas Per Hufleldt, University of Copenhagen, "Factors in Barn Owl natal dispersal: is it density dependence?"

Anna Peterson, University of Minnesota Duluth, "Wind turbine development and conservation of airspace in a major migration corridor."

Stephen Peterson, Utah State University, "Past and present impacts of habitat degradation by Lesser Snow Geese on avian biodiversity along the Hudson Bay lowlands."

Emily Pipher, University of Manitoba, "Effects of grazing intensity and years grazed on songbird nesting success in northern mixed-grass prairies."

John Pourtless IV, Florida State University, "An interpretation of the tenth skeletal specimen of Archaeopteryx."

Christine Rega, University of Delaware, "For-
rest breeding bird response to a multiflora rose invasion: a long term study.”

Taza Schaming, Cornell University, “Occupancy surveys are a reliable survey method for monitoring Clark’s Nutcracker populations.”

Wendy Schelsky, University of Illinois, “Female relatedness to social mate increases cuckoldry and between-year breeding dispersal in a wild bird population.”

Megan Shave, Stonehill College, “Comparative foraging behavior of two generalist tyrant flycatcher (Aves: Tyrannidae) species in Belize.”

David Slager, The Ohio State University, “Movement ecology of Northern Waterthrush (Parkesia noveborcensis) during spring migratory stopover along the upper Mississippi River.”

Maggi Sliwinski, University of Manitoba, “Effect of grazing intensity and duration on songbirds of the mixed-grass prairie.”

K. S. Gopi Sundar, University of Minnesota, “How widespread are ‘common and widespread’ species in the Gangetic floodplains, India.”

Jennifer Thieme, The Ohio State University, “Behavioral and reproductive consequences of nest predator activity to grassland birds.”

Lauren Throop, University of Wyoming, “Evidence for Allee effects? How variation in local tree density influences the mutualism between limber pine (Pinus flexilis) and the Clark’s Nutcracker (Nucifraga columbiana).”

Emily Thomas, Penn State University, “Effect of oil and gas development on songbird abundance in the eastern United States.”

Katerina Tvardikova, University of South Bohemia, “Diversity pattern and significant upward shifts in birds along a complete altitudinal rainforest gradient in New Guinea.”

Andrew Weber, Penn State University, “Habitat use by grassland obligate birds in south-central Pennsylvania.”

Karen Willard, The Ohio State University, “Identifying fine-scale habitat associations for marsh birds using occupancy modeling.”

Jared Wolfe, Louisiana State University, “Gimme’ shelter: a tropical bird’s dissimilar response to global climatic phenomenon in an unbroken forest.”

Selection Committee for the Nice Medal: James D. Rising (Chair), Robert C. Beason, Robert L. Curry, Jerome A. Jackson, and Sara R. Morris; for the Olson Prize: Clait E. Braun (Chair) and Richard C. Banks; for the Klam Service Award: Sara R. Morris (Chair), Richard C. Banks, Robert C. Beason, Robert L. Curry, E. Dale Kennedy, and Jerome A. Jackson; for the Fuertes, Hall/ Mayfield, and Stewart awards: Carla J. Dove (Chair), John Bates, Ramii C. K. Bowie, Jameson E. Chase, R. Terry Cheeser, Greg Farley, Robert C. Faure, James Hare, Kamal Islam, E. Dale Kennedy, Kevin C. R. Kerr, Sarah Kingston, Gustavo A. Londoño, Mark Mallory, Alydolgo G. Navano, Li Jiezena, M. Shane Pruet, Nathan Rice, Scott K. Robinson, Stephan J. Schoch, Elizabeth A. Schreiber, Sarah Sonstagen, Keith Summer, Keith A. Tarvin, Margaret A. Voss, James F. Whatton, Douglas W. White, and Chris Witt; for the Alexander Wilson Prize, the Lynds Jones Prize, and the Nancy Klaam undergraduate presentation awards: Robert C. Beason (Chair), Michael Lombardo, and Susan Skagan; and for the WOS/AFO/COS Travel Awards: Timothy J. O’Connell (Chair), Rolf Koford, and Andrea Townsend.

COMMENDATION

WHEREAS THE ASSOCIATION OF FIELD ORNITHOLOGISTS, THE WILSON ORNITHOLOGICAL SOCIETY, AND THE COOPER ORNITHOLOGICAL SOCIETY met jointly in Kearney, Nebraska, for their 2011 Annual Meetings, hosted by the Tern and Plover Conservation Partnership, and

RECOGNIZING the skill and effort of the Scientific Program Committee, co-chaired by Robert Curry, John McCarty, and Scott Robinson in producing an informative and enjoyable program, including three outstanding plenary lectures, four enlightening symposia on Cerulean Warbler breeding biology and migratory behavior, research on prairie grouse in North America, avian conservation and ecosystem services in agricultural landscapes, and long-term population effects of Piping Plover and Least Tern management on the Great Plains, and a wide array of excellent oral and poster presentations, and

RECOGNIZING the work of the indefatigable Mary Bomberger Brown with support from her assiduous Local Committee, including Christine Thody, Karie Decker, Sara Focke, T. J. Fontaine, Jacki Loonis, Mark Mesarch, and Sarah Rehme to provide an extraordinary venue with comfortable accommodations, state-of-the-art meeting facilities in the brand new Younes Conference
Centre, characteristically warm Nebraskan hospitality, and numerous opportunities for the conferences to interact both professionally and socially, and

RECOGNIZING that our host chose this time and place to coincide with one of the world’s truly great migration phenomena, the staging of innumerable Sandhill Cranes on the Platte River.

THEREFORE BE IT RESOLVED THAT the Association of Field Ornithologists, the Wilson Ornithological Society, and the Cooper Ornithological Society hereby offer their sincere gratitude to all who made this conference an inimitable success.

COMMENDATION

WHEREAS E. DALE KENNEDY has over the past two years served as President of the Wilson Ornithological Society, and

RECOGNIZING that her presidential tenure follows her service to the Society in numerous other capacities, and

RECOGNIZING that under her able leadership the Society has a vibrant and effective committee structure, including a newly reconstituted Conservation Committee, and

RECOGNIZING that under her vision the Society has reaffirmed and deepened its commitment to making the field of ornithology attractive and accessible to students, who represent the future of this discipline, and to that end has overseen significant increases in the substantial financial and honorary incentives that we offer to students,

THEREFORE BE IT RESOLVED THAT the Wilson Ornithological Society offers its sincerest appreciation to E. Dale Kennedy for her leadership and friendship, and looks forward to her continuing contributions to the Society as she begins her new role as Past-President.

BUSINESS MEETING

President E. Dale Kennedy called the Annual Business Meeting to order at 1224 hrs. Thursday, 10 March 2011, in the Chrystal Room of the Younes Conference Centre, Kearney, Nebraska. Noting that the hundreds of members assembled greatly exceeded the required quorum of 25, she introduced Secretary John A. Smallwood, who presented a synopsis of the Council Meeting, which had taken place the previous day. At the end of 2010, the Society’s membership stood at 1,691 individuals, including 250 students. In addition, 254 libraries and institutions subscribed to The Wilson Journal of Ornithology. Secretary Smallwood then asked those assembled to stand in recognition of the following members who were recently deceased: Lawrence Binford (Seattle, WA), Nicholas Collias (Los Angeles, CA), Jurgen Hauffer (Essen, Germany), James Hodges (Davenport, IA), Barrie Hunt (Charleston, IL), Bertram Murray (Somerset, NJ), David Swetland (Miami, FL), J. Daniel Webster (Hanover, IN), Alfred Wehrmaker (Stuttgart, Germany), and Mrs. Elmer Worthley (Finksburg, MD).

Secretary Smallwood reported that the Society enjoys an excellent financial position with an endowment of over $2,500,000 that continues to increase in value as the market improves. On behalf of Council, the Secretary offered sincerest gratitude to the WOS Finance, Audit, and Investment Committee, chaired by Allan Keith, for its perspicacious management of the Society’s funds.

Secretary Smallwood noted that the WOS membership recruitment poster, continually revised and updated by the Membership Committee chaired by Timothy J. O’Connell, was currently on display, and encouraged confeerees who were not yet members to visit said poster and be guided by its influence. Secretary Smallwood further noted that after 5 years of exemplary service, Tim would be retiring from his chairmanship of the Membership Committee.

Secretary Smallwood was delighted to inform those assembled that Council could not be more pleased with the quality and production of The Wilson Journal of Ornithology, and expressed enormous gratitude to our Editor, Clait E. Braun. Further, Council had unanimously re-elected Clait as Editor of The Wilson Journal of Ornithology for Volume 124, 2012. This will be his sixth volume, after which he’s looking forward to being the former Editor of The Wilson Journal of Ornithology. Council has begun its search for the next Editor, who’ll take the reins for Volume 125, 2013.

Finally Secretary Smallwood addressed the issue of proposed changes to the Society’s By-laws that Council had unanimously approved at the 2010 Annual Meeting to place before the membership for a ratification vote at the 2011 Annual Meeting. The following are the proposed changes, as announced at the 2010 Annual Meeting and published in the proceedings of that meeting (The Wilson Journal of Ornithology
BY-LAWS OF THE WILSON ORNITHOLOGICAL SOCIETY

(As Amended 10 March 2011)

ARTICLE I: Name and Objective

Section 1. The organization shall be known as the “Wilson Ornithological Society.” It shall be incorporated under that name as a general not for profit corporation in Illinois. If Illinois should impose new requirements that conflict with the objectives of the Society, the Council, exercising the authority of the Board of Directors of the Corporation, may dissolve the Corporation and reorganize under the laws of another state.

Section 2. The objective of the Wilson Ornithological Society shall be to advance the science of ornithology and the application of science to the conservation of avian species diversity and bird habitats.

ARTICLE II: Membership and Dues

Section 1. The membership of this Society shall consist of four classes: Active Members, Student Members, Life Members, and Honorary Members.

Section 2. Any person may become a member by submitting an application and the amount of dues set by the Council, to the Ornithological Societies of North America (“OSNA”) or other agent delegated by the Council to handle membership administration. Persons desiring to become Life Members shall pay the fee that is then applicable for Life Membership in one lump sum, or may pay in four consecutive annual installments of one quarter of the total amount each.

Section 3. Upon the recommendation of the Council, Honorary Membership may be conferred by the Society by a three-fourths vote at any Annual Meeting. Honorary Members are exempt from dues.

Section 4. All members present may vote on any matter brought before the membership at an Annual Meeting. Any member is eligible to hold an elective office or to be appointed to a committee, subject to the other provisions of these By-laws.

Section 5. All annual dues for the ensuing year shall be due on 1 January. Any member in arrears for dues may be dropped from the roll of members, provided that at least one renewal reminder shall have been sent to such member and the member shall have failed to pay the amount due within ninety days.

Section 6. The Council has the power to expel from membership any person whose conduct is inconsistent with the objectives of the Society, provided that the person shall have been informed in writing of the Council’s concern about the person’s conduct, the person shall have had at least thirty days to respond, and the vote in favor of expulsion shall be by two-thirds of those voting.

ARTICLE III: Officers

Section 1. The officers of this Society shall be a President, a First Vice-President, a Second Vice-President, a Secretary, and a Treasurer. These officers, along with the Editor appointed by the Council, nine persons elected as Councilors, and all living Past-Presidents who are still members of the Society, shall constitute the Council.

Section 2. The President shall preside over meetings of the Council and of the general membership, and shall appoint the chairs and members of committees, except as otherwise specifically set forth in these By-laws.

Section 3. The First Vice-President shall assume the duties of the President when the latter is unable to serve. The First Vice-President shall appoint members to and be in charge of committees presenting awards for student participation in Annual Meetings.

Section 4. The Second Vice-President shall assume the duties of the President when both the President and the First Vice-President are unable to serve. The Second Vice-President shall organize and serve as chair of the Committee for the Scientific Program at the Annual Meeting. The Second Vice-President shall also be responsible, in cooperation with the chair of the local organization that will host the Annual Meeting,
for the production and distribution of the announcement of the Annual Meeting, including the call for papers.

Section 5. The Secretary shall record and distribute minutes of the meetings of the Council and of the general membership, and shall prepare and publish Proceedings of Annual Meetings. In conjunction with the President, the Secretary shall establish agendas for meetings. The Secretary shall assist the President in conducting the business of the Society between Annual Meetings and shall give notice of special or extraordinary meetings.

Section 6. The Treasurer shall be responsible for the financial affairs of the Society, and shall maintain accurate records of monies received and disbursed. The Treasurer shall prepare an annual financial report and a budget proposal for consideration by the Council at its Annual Meeting.

Section 7. The Council of the Society shall conduct the business of the Society. It shall appoint an Editor for The Wilson Journal of Ornithology, and shall fund publication of that journal. It shall approve other necessary expenditures to meet the objectives of the Society. It will hear reports from the Editor and from committees of the Society and take actions as necessary. Nine members shall constitute a quorum of the Council for the conduct of business.

Section 8. The President, First Vice-President, and Second Vice-President shall normally be expected to serve terms of two years, or until their successors are elected. Elected Councilors shall serve terms of three years with terms staggered so that three are elected each year.

Section 9. The five officers and the immediate Past-President shall constitute an Executive Committee for the conduct of business that arises and, as determined by the President, must be resolved between Annual Meetings.

ARTICLE IV: Nominations and Elections

Section 1. The President shall appoint a Nominating Committee at least sixty days prior to the Annual Meeting. Following consultation with those persons being considered for nomination as to their availability to serve and their understanding of the responsibilities of the positions, the Nominating Committee shall nominate at least one person for each position to be filled, and shall report its nominations both to the Council and also to the general membership at the Annual Meeting. Nominations may also be made from the floor at the Annual Meeting by any member in good standing.

Section 2. All officers and members of the Council, except the Editor, shall be elected at the Annual Meeting by a roll call of the members. By the unanimous consent of the members, the Secretary may cast one ballot, representing the vote of the members present.

Section 3. If no Annual Meeting is held in any year, election of officers may be conducted by a mail ballot.

Section 4. Following the completion of two one-year terms in office, the First Vice-President shall be nominated for President and the Second Vice-President for First Vice-President, unless otherwise determined by the Nominating Committee. Terms of office shall begin at the close of the meeting at which the officers were elected.

Section 5. Vacancies occurring because of the death, resignation, or failure of an officer to serve, shall be filled through appointment by the Council, but the person so appointed shall hold office only until the close of the next Annual Meeting of the Society, except in the event of his or her election to that office by the members of the Society at the Annual Meeting following his/her interim appointment.

ARTICLE V: Meetings

Section 1. The Council shall determine the time and place of Annual Meetings of the Society, and such other special or extraordinary meetings as shall be determined necessary by the President in consultation with the Council. Notice of Annual Meetings of the Society shall be sent to all members at least three months in advance of the date of the meetings and shall be given through OSNA's Ornithological Newsletter or through electronic means at least two months prior to the Annual Meeting.

Section 2. The Council shall meet annually prior to the Annual Meeting of the general membership.

Section 3. Twenty-five (25) members shall constitute a quorum for the transaction of business at the Annual Meeting for matters entrusted to action of the membership as a whole.

Section 4. Roberts' Rules of Order shall govern the Society in all cases to which they are applicable and in which they are not inconsistent with the By-laws of the Society.
ARTICLE VI: Financial Matters and Other Resources

Section 1. The Council shall set the amount of the membership dues and the cost of subscriptions to The Wilson Journal of Ornithology.

Section 2. The Council may establish procedures for the recognition of donations to the Society.

Section 3. The establishment and investment of an Endowment Fund and any designated or restricted funds shall be overseen by a Board of Trustees. This Board shall consist of three members appointed by the President and confirmed by the Council.

Section 4. The President shall annually appoint a Library Committee to superintend the accumulation and care of a Wilson Ornithological Society Library.

Section 5. The fiscal year of the Society shall be the calendar year.

ARTICLE VII: Amendments

These By-laws may be amended at any Annual Meeting by a two-thirds vote of the members present or such greater fraction as may be required from time to time by the law of the Society’s state of incorporation, provided that the general substance of the amendment has been proposed at the preceding Annual Meeting or has been recommended by a two-thirds vote of the Council, and a copy has been sent to every member of the Society at least one month prior to the date of action or published in The Wilson Journal of Ornithology at least two months prior to the Annual Meeting. Minor modifications to a proposed amendment may be made in the course of discussion at the Annual Meeting. These By-laws may also be amended by a two-thirds majority of the votes of the members cast by mail ballot or such greater fraction as may be required from time to time by the law of the Society’s state of incorporation, provided that the amendment has been recommended by a two-thirds vote of the Council, and a copy has been sent to every voting member of the Society or published in The Wilson Journal of Ornithology at least two months prior to the date of action. Amendments shall take effect at the close of the meeting at which they are approved or 30 days after the close of a mail ballot.

Secretary Smallwood then gave the floor back to President Kennedy, who summarized the Treasurer’s report, who in turn introduced Editor Braun, who summarized the Editor’s report. The written reports of the Treasurer and the Editor are included below.

Margaret A. Voss, Chair, presented the report of the Nominating Committee, which also included Richard C. Banks and Rebecca J. Safran: President, Robert C. Beason; First Vice-President, Robert L. Curry; Second Vice-President, Sara R. Morris; Secretary, John A. Smallwood; Treasurer, Melinda M. Clark; and members of Council for 2011-2014 (three nominees for three positions), William H. Barnard, Mark E. Hauher, and Margret I. Hatch. Having asked for additional nominations from the floor and hearing none, Chairperson Voss closed the nominations as a result of a motion by Jerome A. Jackson, seconded simultaneously by William E. Davis Jr., and John C. Kricher, which was unanimously passed by acclamation. Jerome Jackson then immediately moved, and was seconded by E. Dale Kennedy, that the Secretary cast a single unanimous vote for the slate of nominees. And again by acclamation, it became so.

President Kennedy returned to the podium to present the WOS Research Awards, including two LOUIS AGASSIZ FUERTES AWARDS, the GEORGE A. HALL/HAROLD F. MAYFIELD AWARD, and the PAUL A. STEWART AWARDS (see above). Sara R. Morris, Chair of the Klamath Service Award Selection Committee, then presented that prestigious award to Charles R. and Leann Blem.

President Kennedy then introduced Second Vice-President Curry, who updated those assembled on the 2012 meeting, at which the Wilson Ornithological Society will participate in the Fifth North American Ornithological Conference in Vancouver, British Columbia, 14-18 August. This meeting will take place on the campus of the University of British Columbia, and Kathy Martin will serve as the chair of the Local Committee.

Having completed the agenda of the Business Meeting, President Kennedy inquired if anyone present had further items of business. Because no one did, Richard C. Banks moved and Jeffrey A. Spedelow seconded that we adjourn. And by the third voice acclamation of this assembly, it came to pass at 1247 hrs.
**REPORT OF THE TREASURER**

**Statements of Revenues and Expenses for the Year Ending 31 December 2010**

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Fuertes 5,000 5,000 5,000
Klamm Service Award 200 1,000 1,000
Wilson, Lynds Jones, Klamm 800 700 700
Student travel grants 4,650 5,000 5,000
Award expenses 2,446 2,553 2,553

Contributions:
Support - Ornith Council $15,000 $15,000 $15,000
Support - Ornith Council, restricted to revision costs (7,500)
Am Bird Conservancy Dues -
AAZN dues 250 250 250
Total Expenses $171,058 $193,203 $192,408
Expenses in excess of revenues before investment income $40,721 $94,073 $88,278

Investment activity:
Revenues
Realized gain/loss - ML $9,191 $27,081 $14,008
Realized gains/losses - Howland (9,288) (20,000) (47,404)
Realized gains/losses - Sutton 31,177 (2,000) (3,033)
Unrealized gain/loss - ML 42,343 (150,000) 216,075
Unrealized gain/loss - Howland 122,318 (200,000) 143,664
Unrealized gain/loss - Sutton (24,544) (40,000) 15,416
Investment earnings - ML 20,545 41,760 23,411
Investment earnings - Howland 34,431 32,695 30,241
Investment earnings - Sutton 4,324 3,673 4,217
Total revenues from investment activity $212,115 $(306,791) $368,579
Investment fees $24,781 $14,366 $20,000
Investment revenues in excess of expenses $187,334 $(321,157) $348,579
Total revenues in excess of expenses $146,613 $(415,230) $360,301

STATEMENT OF FINANCIAL POSITION
31 December 2010
Assets
Cash Investments:
Merrill Lynch - cash $52,800
Cosmetica - Van Tyne checking 424
Van Tyne Univ. Michigan account and PayPal 783
Wilson Editorial bank account 397
Sutton Fund - cash equivalents 2,980
Howland Mgmt - cash equivalent 17,176
Total cash and cash equivalents $74,560
Other Investments:
Merrill Lynch - common stocks 708,845
Merrill Lynch - corp bonds and alternative investment 15,842
Merrill Lynch - mutual funds 108,005
Sutton Fund - equities 142,888
Sutton Fund - corp bonds 10,195
Howland Mgmt - equities 1,235,251
Howland Mgmt - fixed income 311,001
Total Other Investments $2,529,027
Total Assets $2,603,587
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FUND BALANCES

Fund Balances:

Restricted funds - Sutton Fund
Unrestricted funds
Net Income

Fund balance - Klamm

Total Fund Balances

$ 156,063
737,483
146,613
884,096

$ 1,563,428
$ 2,003,587

Melinda M. Clark, Treasurer

EDITOR’S REPORT

We published 858 pages in 2010 which included 118 papers and 24 book reviews as well as the proceedings of the 2010 Annual Meeting, list of reviewers, index, and table of contents for Volume 122. We received 203 new manuscripts and the effective acceptance rate was between 50 and 55%. We have no backlog of manuscripts awaiting publication as ~10-12 remain after each issue make up. My preference is to always have a few carried over as return of revised manuscripts is not uniform. Most manuscripts now arrive electronically as do most reviews. A few referees still prefer to receive and return paper copy.

The number of manuscripts received from outside of North America continues to increase with most from Central and South America. Many of these take substantial work, provided they survive peer review. Considering all manuscripts published in 2010, 47 (40%) involved research from outside of North America (north of Mexico) and 30 (25%) were from Central and South America. This trend appears to be accelerating.

Obtaining reviews is a constant challenge as we may contact up to 12 individuals for each manuscript before reaching agreement with a referee for a review. The review process is the slowest factor affecting reaching a decision. Timely revision of manuscripts by authors is the second reason why manuscripts do not move quickly. I see no easy way to speed up the process, but once revisions are received, we can usually read and return them to authors within 3 days.

We continued the ‘experiment’ of releasing the table of contents prior to printing and shipping of the Journal. Favorable comments far surpass those that either do not care or do not want to receive the TOC before the Journal arrives (85% for, 15% opposed; n = 75+). We are continuing this practice and it may remind ‘members’ to pay their dues when they receive the March TOC.

Serving as Editor involves extensive correspondence related to use of copyrighted material, page charges, and manuscript preparation, as well as the expected activities of tracking manuscripts over periods of 3 to 5+ years. We do not have a large staff (Editor and Editorial Assistant, Book Review Editor, Indexer, and three Editorial Board members for specialized areas). We do detect unethical behaviors including dual publication, plagiarism, and apparent data fabrication. However, these issues are very minor (but can be very problematic).

We have a business model that works well and is professionally supported by personnel of Allen Press. We continue to owe the staff of Allen Press our thanks as they make us appear competent. We also appreciate the support of WOS Council and the Publications Committee. The Wilson Ornithological Society has decisions to consider for moving forward past 2012.

Clait E. Braun, Editor

The reports of the standing committees are as follows:

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The Society continues to be welcoming to students, including undergraduates, especially at Annual Meetings. In addition to a supportive atmosphere, we offer generous travel awards, presentation award opportunities (including the Nancy Klamm Undergraduate Presentation Award, restricted to undergraduates), and both a banquet ticket and a year’s membership for student presenters. Students also compete for research awards (although proposals from graduate students are daunting competition for undergraduates).

Several proposals to improve undergraduate outreach have been discussed at previous Council Meetings clustering around the objectives of (1) mentoring those who would mentor undergradu-
ates, (2) fostering networking among students at meetings, and (3) providing inducements for promising students to form associations with the Society.

Mentoring Ideas

Holding a round table or panel discussion by successful undergraduate mentors on techniques and challenges in fostering student research in ornithology. Topics might include resolving risk management issues, balancing student independence and quality scholarship, and directing undergraduates prior to tenure.

Sharing information on teaching ornithology to undergraduates, including laboratory modules and syllabi.

Supporting faculty who bring undergraduates to national meetings by having the Society send letters of acknowledgement and thanks to deans or provosts at their home institutions.

Networking Ideas

Offering a student bird walk or social event during the day early in a meeting. Invite amateur ornithologists, if available, to mix with students.

Encourage students to attend Society Business Meetings through creative scheduling as at Kearney.

Potential Further Inducements

Encouraging Fuertes and Stewart award winners to present results of their work at a Wilson meeting by giving preference in travel grants or offering separate travel funds.

The web site for the Society offers information on graduate programs in ornithology as a service to interested undergraduates. In the past months, several students contacted me by e-mail with questions and suggestions after using the WOS home page. Centralized and up-to-date information on summer and other research opportunities for beginning students are available elsewhere on the web. My information on graduate programs is stale, and the WOS home page is not impressive or "sticky." Given the maturity of the web and competition from other sites, how much effort should WOS direct to its web site?

Douglas W. White, Chair

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

The following statistics attest to the work done by Janet Hinshaw and others on our behalf as staff for the WOS library (Van Tyne Library at the University of Michigan, Museum of Zoology).

Acquisitions

Exchanges.—We received 119 publications by exchanges with 95 organizations or individuals. We have lost several exchanges in the past few years and subscribed to several to keep them current.

Gifts.—We received 26 publications as gifts from 23 organizations.

Subscriptions.—We also received 31 publications from 23 subscriptions, spending a total of $997.08 on subscriptions in 2010.

Donations.—Donations received included 215 items from the World Museum, Liverpool; the South African Ornithological Society; and The Peregrine Fund.

Purchases.—The library purchased 26 journal volumes and 11 books, for $459.26.

Dispersals

Sales.—Five books were sold, bringing in a total of $70.

Gifts to Other Institutions.—In an effort to reduce our inventory of back issues of The Wilson Bulletin, issues were offered to interested organizations. Of 1,334 journal issues donated to three organizations, 11 went to the South African Ornithological Society, 661 to Northern Michigan University, and 662 to The Peregrine Fund.

Use of Resources

During the past year 15 loans of 62 books, and photocopies and scans of articles were sent to 12 members. We remind members that we can lend books or provide paper or electronic copies of articles from items in the library.

Thank Yous

I thank our student library worker, Theresa Gorman, for day-to-day operations and our secretary, Fritz Paper, for assistance with photocopying. I thank Janet Hinshaw for providing these data for us and for the efficient and important work she is doing for us and the greater ornithological community.

Jerome A. Jackson, Chair

REPORT OF THE SCIENTIFIC PROGRAM COMMITTEE

The Committee on the Scientific Program consisted of WOS Second Vice-President Robert

PAPER SESSIONS

Symposium: Cerulean Warbler Breeding Biology and Migratory Behavior


Kamal Islam, Ryan Dihala, Kyle Kaminski, Margaret MacNeil, Jennifer Wagner, and Lila (Prichard) Young, Ball State University, "The Hardwood Ecosystem Experiment: do silvicultural treatments affect Cerulean Warbler relative abundance and territory size and placement in southern Indiana?"


Christopher M. Rogers, Wichita State University. "Season-long fecundity, brood parasitism, and nest predation in the Cerulean Warbler in southwestern Michigan."


Scott H. Stoleson, USFS Northern Research Station, Jeffery L. Larkin, Indiana University of Pennsylvania, David Buehler and Patrick Keyser, University of Tennessee, Paul Hamel, USFS Southern Research Station, Amanda Rodewald, The Ohio State University, and Petra B. Wood, USGS West Virginia Cooperative Fish and Wildlife Research Unit, "From research to management: development of best management practices for Cerulean Warblers."


Symposium: Research on Prairie Grouse in North American

Cameron L. Aldridge and D. Joanne Saher, Colorado State University, Theresa M. Childers


Clait E. Braun, Grouse Inc., and K.C. Jensen, South Dakota State University, "Introduction: overview of status and conservation concerns for prairie grouse in North America."

Rob Channel I and Greg Farley, Fort Hays State University, "Analyses of the distribution and population trends of Lesser Prairie-Chicken with reference to Kansas populations."

Robert M. Gibson, University of Nebraska-Lincoln, "The effect of hunting on population size in Greater Sage-Grouse."

Andrew J. Gregory, L. B McNew, B. K. Sandercock, and S. M. Wisely, Kansas State University, "Multiple paternity and conspecific brood parasitism among Greater Prairie-Chickens: a conditional strategy for coping with anthropogenic landscape disturbance?"


Sara J. Oyler-McCance and Jennifer A. Fike, USGS Fort Collins Science Center, and Michael Phillips and Paul Lukacs, Colorado Division of Wildlife, "Use of molecular tagging to estimate demographic parameters in Gunnison Sage-grouse."

Travis J. Runia and Kent C. Jensen, South Dakota State University, "Impacts of Conservation Reserve Program (CRP) and landscape composition on presence and density of prairie grouse leks in South Dakota."

**Symposium: Avian Conservation and Ecosystem Services in Agricultural Landscapes**

Julie A. Jedlicka, University of California, Santa Cruz, Russell Greenberg, National Zoological Park, and Deborah K. Letourneau, University of California, Santa Cruz, "Conservation of avian species strengthens ecosystem services in California vineyards."

John P. McCarty, University of Nebraska at Omaha, Joel G. Jorgensen, Nebraska Game and Parks Commission, and L. LaReesa Wolfenbarger, University of Nebraska at Omaha, "Buff-breasted Sandpiper (Tringa brevipes) use of agricultural fields in the Rainwater Basin, Nebraska, and implications for conservation."

Larkin A. Powell, University of Nebraska-Lincoln, "Cross-property agreements on ranch lands provide scale for avian conservation."

John E. Quinn, University of Nebraska-Lincoln, Ron J. Johnson, Clemson University, and James R. Brandle, University of Nebraska-Lincoln, "Avian conservation in temperate agroecosystems: consideration of spatial scale and management outcomes."

Benjamin S. Rashford and Eric Cropper, University of Wyoming, and Richard Voldseth, North Dakota State University, "Climate change, agriculture and wetlands: implications for waterfowl conservation in the Prairie Pothole Region."

**Symposium: Long-term Population Effects of Piping Plover and Least Tern Management on the Great Plains**


Joy Felio, Daniel Catlin, and James Fraser, Virginia Tech., "Colonization and abandonment of Missouri River sandbars by breeding Piping Plovers."

Joel G. Jorgensen, Nebraska Game and Parks Commission, and Mary Bomberger Brown, Tern and Plover Conservation Partnership, "Interior Least Terns and Northern Great Plains Piping Plover nesting on natural and human-created habitat in the Lower Platte River: implications for species and river management."

Erin A. Roche, University of Tulsa, and Terry L. Shaffer, Michael J. Anteau, Mark H. Sherfy, Marsha A. Sovada, Jennifer H. Stucker, and Mark T. Wiltermuth, USGS Northern Prairie Wildlife Research Center, "Do you see what I see? Detecting Least Tern and Piping Plover fledglings on the Missouri River."

Terry L. Shaffer, Mark H. Sherfy, Michael J. Anteau, Jennifer H. Stucker, and Marsha A. Sovada, USGS Northern Prairie Wildlife Research Center, and Erin A. Roche, University of...
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Tulsa. “Status and trends of Missouri River Least Terns and Piping Plovers: how much do we know?”

General Sessions
Aubrey Alamshah and Edward H. Burtt Jr., Ohio Wesleyan University. “Seasonal variation in the maintenance behavior of House Sparrows, Passer domesticus.”
Amber Albores and Jeffery P. Hoover, University of Illinois at Urbana-Champaign and Institute of Natural Resource Sustainability, Illinois Natural History Survey. “Cowbird parasitism increases after high fledging success of cowbird, but not host, nestlings.”
Catherine Alsford, Brynne Slumpe, and Sara Morris, Canisius College, and Lindsey Walters, Northern Kentucky University. “Breeding biology of a newly-established population of House Wrens.”
Amy K. Amones and Michael J. Lanzone, Powdermill Avian Research Center, and Andrew J. Farnsworth, Cornell Laboratory of Ornithology. “A novel method to study inter- and intraspecific variation of flight-calls in captivity.”
Todd W. Arnold and Robert M. Zink, University of Minnesota. “Collisions with buildings and towers do not affect long-term avian population trends.”
Amanda V. Bakian and Kimberly A. Sullivan, Utah State University. “The use of aquatic and terrestrial insects by Willow Flycatchers at Fish Creek, Utah, revealed by carbon and nitrogen stable isotopes.”
Gina Barton and Brett K. Sandcock, Kansas State University. “Long-term changes in the stopover dynamics of migratory songbirds in northern California.”
Tyler J. Beck and Dale E. Gawlik, Florida Atlantic University, and Elise V. Pearlstine, University of Florida. “The avian community response to constructed treatment wetlands for Everglades restoration.”
Doug Becker, James Sheehan, and Petra Bohall Wood, USGS West Virginia Cooperative Fish and Wildlife Research Unit, and Harry Edenborn, USDE National Energy Technology Laboratory. “Preliminary effects of Marcellus shale drilling on Louisiana Waterthrush in West Virginia.”
James M. Beersens, Dale E. Gawlik, and Erik Noonburg, Florida Atlantic University. “Modeling flexible habitat selection of wading birds in dynamic wetlands.”
Thomas J. Benson, University of Illinois, Nicholas M. Anich, Wisconsin Department of Natural Resources, Ashland, and James C. Bednarz, Arkansas State University. “Effects of habitat structure and song playbacks on detection probability of Swainson’s Warblers: implications for survey design.”
Brian J. Biehlert, Texas A&M University-Kingsville, Andrea R. Litt, Montana State University, and Fred C. Bryant, Leonard A. Brennen, and Tom Langschied, Texas A&M University-Kingsville. “Are wintering grounds for grassland birds threatened by a native invasive grass?”
Jennifer A. Blakesley, Rocky Mountain Bird Observatory, Jay D. Carlisle, Idaho Bird Observatory, and Steven J. Slater, HawkWatch International. “Site occupancy by Flammulated Owls: a pilot study in three states.”
David Bonter, Benjamin Zuckerberg, and Carolyn Sedgwick, Cornell University. “Daily feeding patterns in winter: predation pressure may not be driving behavior.”
Bryan A. Botson, Dale E. Gawlik, and Joel C. Trexler, Florida Atlantic University. “Modeling trophic linkages with wading bird prey concentrations: turning ecosystem attributes into wading bird food.”
Reed Bowman, Archbold Biological Station. “Variation in population density and territory size across a spatio-temporal urban gradient.”
Eli S. Bridge, Jeffrey F. Kelly, Nyambayar Battbayar, and Xiangming Xiao, University of Oklahoma, and John Y. Takekawa, Kyle A.
Spragens, and Nichola J. Hill, USGS Western Ecological Research Center, "Tracking avian influenza with stable isotopes."

Christopher W. Briggs and Michael W. Collopy, University of Nevada, Reno. and Brian Woodbridge, U.S. Fish and Wildlife Service, "Natal dispersal of Swainson’s Hawks in Butte Valley, California."

Jessi L. Brown and Michael W. Collopy, University of Nevada, Reno. "Reproductive decisions by the American Kestrel: experimental evidence that female kestrels exhibit a fixed level of investment in offspring."

Todd J. Buckley, Felipe Chavez-Ramirez, Larkin A. Powell, and Andrew J. Tyre, University of Nebraska-Lincoln. "Modeling the effect of landscape and environmental factors on Sandhill Crane distribution in the central Platte River Valley of Nebraska."

Jeffrey J. Buler, University of Delaware, and Deanna K. Dawson, USGS Patuxent Wildlife Research Center, "Weather radar analysis of landbird stopover sites during fall migration in the northeastern U.S."

Curtis W. Burney, Air Force Research Laboratory, and David W. Winkler, Cornell University, "The temporal and spatial dynamics of swallow roosts found in the eastern and central United States."

Edward H. Burtt Jr., George S. Hamaoui, and Max R. Schroeder, Ohio Wesleyan University, "Dark plumage to resist bacterial degradation: facultative or evolutionary response?"

Matthew D. Carling, University of Wyoming, "Genetics of speciation: insights from Passerina buntings."

Erin B. Cashion and Paul G. Rodewald, The Ohio State University. "Migrant landbird use of natural and restored riparian forest habitats in agricultural landscapes during stopover."

Jameson F. Chace, Salve Regina University, Thomas LaPointe and Rachel Cliche, Silvio O. Conte National Fish and Wildlife Refuge, and Leslie Moffat, Middlebury College, "Breeding bird responses to American Woodcock habitat management in northeastern Vermont."


Scott J. Chiavacci and James C. Bednarz, Arkansas State University, "Multi-scale temporal variation in prey deliveries at Mississippi Kite nests."

William S. Clark, Harlingen, TX, "Harlan’s Hawks differ in adult plumage and a leg measure from Red-tailed Hawks."

Peter S. Coates, Michael L. Casazza, Brian J. Halstead, and Joseph P. Hleskes, USGS Western Ecological Research Center, and James A. Laughlin, USDA California Wildlife Services, "Using avian radar to examine time-dependent effects on avian activity and relationships with meteorological factors."

Reesa Yale Conrey and Susan K. Skagen, USGS Fort Collins Science Center, and Victoria J. Dretz, Colorado Division of Wildlife, "Precipitation and temperature influence nest survival of shortgrass prairie birds."

Andrea Cornina and Jeff Kelly, University of Oklahoma, "Preliminary genetic analysis of the Painted Bunting Passerina ciris in South West Oklahoma."

Melissa Creasey and Erica Nol, Trent University, and Dawn Burke, Ontario Ministry of Natural Resources, "The effects of selection harvesting on Black-throated Blue Warbler reproduction."

C. M. Curry and M. A. Patten, University of Oklahoma, "Song varies across older and younger hybrid zones in Black-crested (Baeolophus atricapillus) and Tufted (B. bicolor) titmice."


Anthony C. Dalisio and William E. Jensen, Emporia State University, and Timothy H. Parker, Whitman College, "Song dialects in alpine-breeding birds of the Rocky Mountains."

Amy J. Davis, Phillip Street, and Paul Doherty, Colorado State University, and Mike Phillips, Colorado Division of Wildlife, "Habitat effects on nesting success of Gunnison Sage-Grouse, Centrocercus minimus, in Gunnison, Colorado."

Nicole M. Davros, Jeffrey D. Brawn, and Jeffrey P. Hoover, University of Illinois at Urbana-Champaign, "An experimental test of density-dependent reproduction in Prothonotary Warblers, Protonotaria citrea."

Roi Dor, Caren B. Cooper, Irby J. Lovette, and...
David W. Winkler, Cornell University. “Clock gene variation in swallows.”
Matthew B. Dugas, University of Oklahoma. “Environmental and parental effects explain among-brood differences in ornamental mouth coloration of nestling House Sparrows, Passer domesticus.”
Heidi J. Erickson and Cameron L. Aldridge, Colorado State University. “Effects of prescribed fire and timing of summer livestock grazing on avian habitat selection in a high-elevation sagebrush ecosystem.”
Chris Foote, Lubna Nasir, and Pat Monaghan, University of Glasgow. “Telomere length is linked to early life conditions and survival in long-lived seabirds.”
Alexandra Frohberg and Keith Geluso, University of Nebraska at Kearney and Mary Harner, University of Nebraska at Kearney and the Platte River Whooping Crane Maintenance Trust. “Testing a long-standing ecological principle: the hemi-marsh condition hypothesis.”
Jeff Garcia and Craig W. Benkman, University of Wyoming. “Cascading trait-mediated indirect effects across the boreal forest.”
Thomas Gardali, Nathaniel E. Seavy, and Ryan T. DiGaudio, PRBO Conservation Science, and Lyaan A. Comrack, California Department of Fish and Game. “Integrating climate vulnerability into the California Bird Species of Special Concern list.”
Dale E. Gawlik, Florida Atlantic University, Garth Herring, University of California, Davis, James M. Beerens, Samantha M. Lantz, and Bryan Botson, Florida Atlantic University, and Mark I. Cook and Rachael Pierce, South Florida Water Management District. “A synthesis of recent studies showing how prey availability affects wading bird habitat selection, physiology, and reproduction.”
Richard E. Gibbons, Louisiana State University, Javier Barrio, Centro de Ornitolgía y Biodiversidad (CORBIDI), Urb. Huertos de San Antonio, Lima 33, Peru, Gustavo Bravo, Louisiana State University, and Luis Alza, Centro de Ornitolgía y Biodiversidad (CORBIDI), Lima, Peru. “Do new distributional records represent vagrancy or the typical range? Testing for climatic niche equivalency using extralimital and winter range occurrence records of Black-fronted Ground-Tyrant (Muscisaxicola frontalis).”
Elizabeth A. Gow and Karen L. Wiebe, University of Saskatchewan. “Female Northern Flickers increase parental care but males don’t during temporary brood enlargements.”
Cory Gregory and Stephen J. Dinsmore, Iowa State University, Larkin A. Powell, University of Nebraska-Lincoln, and Joel G. Jorgensen, Nebraska Game and Parks Commission. “Estimating the abundance of Long-billed Curlews in Nebraska.”
Blake Grisham and Clint Boal, USGS Texas Cooperative Fish and Wildlife Research Unit, and David Haukos, USFWS, Texas Tech University. “Thermal tolerances of nesting Lesser Prairie-Chickens and the potential population level influence of climate change.”
Tyler M. Harms and Stephen J. Dinsmore, Iowa State University. “Habitat associations of secretive marsh-birds in Iowa.”
Matthew A. Hayes, University of Wisconsin, and Jeb A. Barzen, International Crane Foundation. “Mate and site fidelity of breeding Sandhill Cranes in a dense population in Wisconsin.”
Christopher M. Heckscher and Syrena M. Taylor, Delaware State University, and James W. Fox and Vsevolod Afanasyev, Environment Research Council, Cambridge, UK. “Veery wintering locations and intratropical migration: results from geolocator tracking.”
Steven C. Hess, USGS Pacific Island Ecosystems Research Center, Christina Cornett, Hawaii Cooperative Studies Unit and Hawaii National Park, Kathleen Misajon, Hawaii National Park, and John J. Jeffrey, Pepeekeo, HI. “Tracking movements of the endangered Hawaiian Goose with satellite telemetry.”
Kyle G. Horton and Sara R. Morris, Canisius College, and Amy Amores and Michael Lanzone, Powdermill Avian Research Center, "Flight calls in wood-warblers: Do migrants respond to conspecific calls?"

Peter A. Hosner and Robert G. Moyle, University of Kansas, "Testing the Pleistocene aggregate island complex (PAIC) model of diversification in co-distributed avian lineages."

Kristy B. Howe and David J. Delechanty, Idaho State University, and Peter S. Coates, USGS Western Ecological Research Center, "Selection for anthropogenic structures and vegetation characteristics by Common Ravens (Corvus corax) within a sagebrush-steppe ecosystem."

Joanna K. Hubbard, Brittany R. Jenkins, and Rebecca J. Safran, University of Colorado, "Heritability of a sexually selected melanin-based trait in North American Barn Swallows, Hirundo rustica erythropus."

Pamela Hunt, New Hampshire Audubon, "Using auditory detections to assess habitat use in the Eastern Whip-poor-will (Caprimulgus vociferus)."

Allison K. Jackson, Sarah B. Folsom, and David C. Evers, Biodiversity Research Institute, Anne M. Condon and John Schmerl, U.S. Fish and Wildlife Service, and Daniel A. Cristol, College of William and Mary, "Mercury footprint extends far downstream for songbirds along the South Fork Shenandoah River."

Jerome A. Jackson and Bette J. S. Jackson, Florida Gulf Coast University, "Functional morphology of the bill in the Anhingidae: an adaptation that can be maladaptive in the modern world."

Frances C. James and John A. Pourtless IV, Florida State University, "Character support for the hypothesis that birds are maniraptoran theropod dinosaurs."

Allison E. Johnson, University of Chicago, and Steve Freedberg, St. Olaf College, "Facial markings may serve as a kin recognition cue in juvenile Cliff Swallows (Petrochelidon pyrrhophona)."

Erik I. Johnson and Philip C. Stouffer, Louisiana State University, "Ectoparasites reduce feather growth in an Amazonian forest bird, Willisiornis poecilinota."

Cara Joos, University of Missouri, Frank R. Thompson III, USFS Northern Research Station, and John Faaborg, University of Missouri, "Settlement order and productivity of Bell’s Vireos (Vireo bellii bellii)."

Christopher F. Jorgensen and Joseph J. Fontaine, USGS Nebraska Cooperative Fish and Wildlife Research Unit, and Larkin Powell, University of Nebraska-Lincoln, "Assessing landscape and habitat attributes at multiple scales: what drives avian abundance and distribution in grasslands?"

Stephanie A. Kane, Fort Hays State University, "Effects of multiple habitat management practices on breeding habitat usage by Eastern Black Rail."

Allison Karlhen Lang and Eric K. Bollinger, Eastern Illinois University, "The effect of host to parasite egg ratio on cowbird egg ejection by American Robins."

Laura J. Kearns and Amanda D. Rodewald, The Ohio State University, "Influence of prior fate and nest predator community on nestling decisions of multi-brooded forest songbirds."

Jeff Kelly, Ryan Shipley, Ken Howard, Phl Chilson, Wilfred F. Frick, and Thomas H. Kunz, University of Oklahoma, "A national scale analysis of Purple Martin pre-migratory roost formation using weather surveillance radar."

S. D. Keyan and C. E. Trainor, Environquest Ltd., "Carbohydrate analysis of berries available for foraging by birds."

Daniel Kim, Portland State University, "Effects of severe weather to reproductive success of hosts and brood parasites."

Rebecca Kirby and Mark E. Berres, University of Wisconsin, "Conservation genetics of the White-tailed Sabrewing (Campylopterus ensipennis) on Tobago, West Indies."

Eileen M. Kirsch and Brian R. Gray, USGS Upper Midwest Environmental Sciences Center, and Sherwin Toribio, University of Wisconsin-La Crosse, "Possible effects of an invasive plant, reed canary grass (Phalaris arundinacea), on the breeding bird assemblage in Upper Mississippi River floodplain forest."

Jessica A. Klassen, Florida Atlantic University, "Canopy characteristics affecting avian reproductive success: the Golden-cheeked Warbler."

Linda A. Lait and Theresa M. Burg, University of Lethbridge, "The genetic makeup of the Boreal Chickadee: using mtDNA and microsatellites to discern the population structure of a small boreal songbird."

Diane V. Landoll, Michael S. Husak, and Michael T. Murphy, Portland State University, and Jeff Kelly, University of Oklahoma and Cameron University, "Extra-pair paternity and morphological correlates in the Scissor-tailed Flycatcher (Tyrannus forficatus) in southwestern Oklahoma."


Carly N. Lapin, Matthew A. Etterson, and Gerald J. Niemi, University of Minnesota, "Breeding habitat of the rare Connecticut Warbler (Oporornis agilis) is related to patch size."

Adrienne J. Leppold and Rebecca L. Holberton, University of Maine, "The Gulf of Maine migration mystery: filling in the gaps."

Iris L. Levin and Patricia G. Parker, University of Missouri-St. Louis, Whitney R. Harris World Ecology Center, and the WildCare Center, "The Gulf of Maine migration mystery: filling in the gaps."


Teresa J. Lorenz, University of Idaho, and Kimberly A. Sullivan and Amanda V. Bakian, Utah State University, "Spring-summer space use by Clark's Nutcrackers in Washington State."


Monika Maier and Kimberly Sullivan, Utah State University, "Not just a walk in the park: Clark's Nutcracker in declining habitat."

Katherine McCarville, Upper Iowa University, "A new interpretation for the classical avian fossil locality at Fossil Lake, Oregon."

Chris McCreedy and Charles van Riper, University of Arizona, "Drought-delay impacts on Black-tailed Gnateater Polioptila melanura and Verdin Auriparus flaviceps productivity in the Sonoran Desert."

David B. McDonald and Dai Shizuka, University of Wisconsin, "A social network approach to dominance."

Bailey D. McKay, Herman L. Mays, Yuchun Wu, Hui Li, Yao Cheng-te, Isao Nishiumi, and Fusheng Zou, University of Minnesota and Bell Museum, "The challenge of delimiting recent lineages: the Chinese/Taiwan Bulbul (Pycnonotus sinensis/lavanus) complex as a case study."

Matt McKim-Louder and Jeffrey P. Hoover, University of Illinois at Urbana-Champaign and Institute of Natural Resource Sustainability, Illinois Natural History Survey, "Assessing the effects of season, brood parasitism, and individual quality on first-year apparent survival in a neotropical migratory songbird."


Robert K. Murphy and Gregory W. Wright, University of Nebraska at Kearney, and Arun K. Pandey, EDM International Inc., "Mortality of migrant Sandhill Cranes at power lines over the Platte River, central Nebraska."

Mduduzi Ndlovu, Graeme Cumming, and Phil Hockey, University of Cape Town, "Phenotypic flexibility in African warfowl."


Carl H. Oliveros, Isla Biodiversity Conservation and University of Kansas, and Cynthia Adeline A. Layusa and Jameson B. Reyon, Isla Biodiversity Conservation, Las Pinas City, Philippines, "Monitoring the population of the Calayan Rail."

Joseph C. Ortega and Catherine P. Ortega, Fort Lewis College, "Contributing variables to nest
survival, and the breeding biology, of the Western Wood-Pewee (Contopus sordidulus), a habitat generalist, in southwest Colorado."

Jessica A. Oswald, University of Florida, "Late Pleistocene passerines of the Talara tar seeps in northwest Peru: indicators of climate change."

David L. Otis, USGS Iowa Cooperative Fish and Wildlife Research Unit, and David A. Miller, USGS Patuxent Wildlife Research Center, "Trade-offs in vital rates of Mourning Doves, Zenaida macroura."

Jamie L. Palmer, Thomas F. McCutchan, Sharon L. Deem, Dan Hartman, and Patricia G. Parker, University of Missouri-St. Louis, "Sero-prevalence of malarial antibodies in Galapagos Penguins (Spheniscus mendiculus)."

Timothy H. Parker, Whitman College, "Meta-analysis in a model species suggests plumage color may not be a signal of individual quality influencing mate choice."

David C. Pavlacky Jr., Jennifer A. Blakesley, and David J. Hanni, Rocky Mountain Bird Observatory, "Hierarchical occupancy estimation and multi-scale habitat use of Brewer’s Sparrows in the Southern Rockies/Colorado Plateau Bird Conservation Region."

Brian D. Peer, Western Illinois University, and Robert A. McCleery, University of Florida, "Adaptive modulation of cowbird host defensive behavior in relation to its cost and the likelihood of parasitism."

Mario B. Pesendorfer, University of Nebraska-Lincoln, and Scott Sillett, National Zoological Park, "Scatter-hoarding of acorns by Island Scrub-Jays, Aphelocoma insularis, on Santa Cruz Island."

Margaret R. Petersen, David C. Douglas, and Sarah McCloskey, USGS Alaska Science Center, and Heather Wilson, U.S. Fish and Wildlife Service, "Interannual winter site fidelity evident among most Pacific Common Eiders breeding in northwest Alaska."

Michelle L. Petersen and Dale E. Gawlik, Florida Atlantic University, and Mark I. Cook, South Florida Water Management District, "Foraging habitat parameters: preferences of Everglades wading birds."

Anna C. Peterson and Gerald J. Niemi, University of Minnesota, "Wind turbine development and conservation of airspace in a major migration corridor."

Stephen L. Peterson, David N. Koons, and Robert F. Rockwell, Utah State University, "Past and present impacts of habitat degradation by Lesser Snow Geese on avian biodiversity along the Hudson Bay Lowlands."

Martin J. Pfeiffer, Carson National Forest, and Anna M. Pidgeon, University of Wisconsin-Madison, "Effects of recreational trails on passerine abundance and nest success in southern Wisconsin forests."

Emily N. Pipher and Nicola Koper, University of Manitoba, "Effects of grazing intensity and years grazed on songbird nesting success in northern mixed-grass prairies."

John A. Pourlous IV and Frances C. James, Florida State University, "An interpretation of the tenth skeletal specimen of Archaeopteryx."

Christine Rega and W. Gregory Shriver, University of Delaware, and Vince D’Amico, U.S. Forest Service NRS-04, University of Delaware, "Forest breeding bird response to a multiflora rose invasion: a long term study."

Sarah E. Rehtne and Craig R. Allen, University of Nebraska-Lincoln, Keith A. Hobson, Environment Canada, Saskatoon, and Larkin A. Powell, University of Nebraska-Lincoln, "Can nestling songbirds reveal adult breeding site fidelity?"


Aleix Richardson and Nicola Koper, University of Manitoba, "Changes in the songbird community since time burned in grazed and ungrazed pastures."

Vanya G. Rohwer and Paul R. Martin, Queen’s University, "Fitness consequences and selective mechanisms favoring local nest morphologies in Yellow Warblers: nest transplant experiments between subarctic and temperate populations."

Eric J. Ross, California State University-Monterey Bay, Derek M. Schook, Colorado State University, Susan E. Alexander and Fred G. R. Watson, California State University-Monterey Bay, and Timothy H. Parker, Whitman College, "Geographic structure of song sharing in the Dickcissel (Spiza americana) determined by cross correlation."

Kristen Ruegg, University of California, Los Angeles, "Migratory connectivity in the age of genomics."

Janet M. Ruth, USGS Fort Collins Science Center, and Robert R. Diehl and Rodney K. Felix Jr., University of Southern Mississippi, "Bird
migration and stopover habitat use in the South‐
west.”

Victoria Saab, USFS Rocky Mountain Research
Station. Erin Towler, National Center for Atmo-
sphere Research, and Karen Newlon, Montana
Natural Heritage Program. “Temperature effects
on daily survival rates of nesting Lewis’s
Woodpeckers Melanerpes lewis in the past,
present, and future.”

Rebecca J. Safran, University of Colorado,
“The dynamics of physiology-trait relationships:
implications for honest signal theory.”

Wendy M. Schelisky and Jeffrey P. Hoover,
University of Illinois at Urbana-Champaign, and
Scott K. Robinson, University of Florida. “Fe-
nale relatedness to social mate increases cuck-
oldy and between-year breeding dispersal in a
wild bird population.”

Megan Shave, Stonehill College, and John
Kitcher, Wheaton College. “Comparative forag-
ing behavior of two generalist tyrant flycatcher
(Aves: Tyrannidae) species in Belize.”

Daisaburo Shizuka, University of Chicago,
Oscar Johnson and David Moldoff, University of
California, Santa Cruz. Alexis Chaine, Station
d’Ecologie Experimentale du CNRS, Moulis,
France, and Bruce E. Lyon. University of
California, Santa Cruz. “Social structure of
wintering migrant sparrows: a social network
approach.”

W. Gregory Shriver, University of Delaware,
Kathleen M. O’Brien, Rachel Carson National
Wildlife Refuge, Mark Ducey, University of New
Hampshire, and Thomas P. Hodgman, Maine
Department of Inland Fisheries and Wildlife.
“Long term changes in Saltmarsh Ammodramus
caudacitus and Nelson Ammodramus nelsoni
sparrow abundance at Rachel Carson National
Wildlife Refuge, Maine, USA.”

David L. Slager and Paul G. Rodewald, The
Ohio State University, and Patricia J. Heglund,
"Exotic vegetation and altered disturbance re-
regimes in New Mexico riparian forests: response
by Black-chinned Hummingbirds.”

Julie W. Smith, Stephanie M. Sjoberg, Matthew
C. Mueller, and Craig W. Benkman, University of
Wyoming. “Assortative flocking in crossbills and
implications for ecological speciation.”

Jason F. Smyth and Christin L. Pruett, Florida
Institute of Technology, and Kevin Winker,
University of Alaska Museum. “A Bayesian
model of island colonization based on Song
Sparrow (Melospiza melodia) populations in the
Aleutian Islands of Alaska.”

Helen R. Sofaer and Kathryn M. Langin,
Colorado State University. T. Scott Sillett,
National Zoological Park, and Cameron K.
Ghalambor, Colorado State University. “Density
dependence in two seasons: demographic effects
of competition and climate.”

Robert A. Sparks and David J. Hanni, Rocky
Mountain Bird Observatory. “Hierarchical dis-
tance sampling models.”

Jeffrey A. Spedelowe, James E. Hines, and
James D. Nichols, USGS Patuxent Wildlife
Research Center. Ian C. T. Nisbet, I.C.T. Nisbet
and Company, Carolyn S. Mostello, Massachu-
setts Division of Fisheries and Wildlife, Grace
Cormons, Great Gull Island Project. Helen Hays,
Great Gull Island Project and American Museum
of Natural History, and Jeremy J. Hatch, Univer-
sity of Massachusetts. “Estimating adult breeding
dispersal/fidelity at different geographic scales to
evaluate restoration efforts for Roseate Terns.”

Brynne A. Stumpe, Catherine C. Alsford, and
Sara R. Morris, Canisius College. “Does House
Wren singing rate change with stage in breeding
cycle?”

Ryan J. Stutzman, Susan K. Skagen, and Joseph
J. Fontaine, USGS Nebraska Cooperative Fish and
Wildlife Research Unit and USGS Fort Collins
Science Center, “Avian migration in the face of
an altered landscape.”

Kimberly A. Sullivan and Leslie J. Brown,
Utah State University. “The response of breeding
passerines to rangeland alteration.”

K. S. Gopi Sundar, University of Minnesota,
“How widespread are “common and wide-
spread” species in the Gangetic floodplains,
India?”

David L. Swanson, University of South Dakota,
“Ultrasonographic detection of seasonal changes
in flight muscle size in small birds.”

Jason Thiele and Charles Dieter, South Dakota
State University, and Kristel Bakker, Dakota State University, “Distribution and habitat selection of the Western Burrowing Owl (Athene cunicularia hypugoea) in western South Dakota.”

Emily H. Thomas, Margaret C. Brittingham, and Walter M. Tzilkowski, Penn State University, and Scott H. Steleson, USFS Northern Research Station, “Effect of oil and gas development on songbird abundance in the eastern United States.”

Lauren E. Throop and Craig W. Benkman, University of Wyoming, “Evidence for Allee effects? How variation in local tree density influences the mutualism between limber pine (Pinus flexilis) and the Clark’s Nutcracker (Nucifraga columbiana).”

Romeo Tinajero and Ricardo Rodríguez-Es trella, Centro de Investigaciones Biológicas de Noroeste (CIBNOR), La Paz, Baja California Sur, México, and Jesús A. Lemus and G. Blanco, Museo Nacional de Ciencias Naturales (CSIC), c/ José Gutierrez Abascal 2, 28006 Madrid, Spain, “Effects of habitat fragmentation on the community of pathogens of the Harris’ Hawk in the desert of Baja California Sur, México.”

Lauren F. Tingco, California State University, Los Angeles, “Impact of disturbance on the roosting behavior of Western Snowy Plovers, (Charadrius alexandrinus nivosus).”

Katerina Tvardikova and Vojtech Novotny, University of South Bohemia and Institute of Entomology, Ceske Budejovice, Czech Republic, “Diversity pattern and significant upward shifts in birds along a complete altitudinal rainforest gradient in New Guinea.”

Jonathon J. Valente, Richard A. Fischer, Michael P. Guilfoyle, and Sam S. Jackson, U.S. Army Engineer Research and Development Center, Michael D. Kaller, Louisiana State University Agricultural Center, and John T. Ratti, University of Idaho, “Bird community response to vegetation cover and composition in riparian habitats dominated by Russian olive (Elaeagnus angustifolia).”


Carol Vleck, David Vleck, and Christopher Foote, Iowa State University, and David Winkler, Cornell University, “Effects of carrying an instrument package on telomere length and innate immune function in Tree Swallows.”

Kristin Wakeland, Patrick Mathews, and Alan Macarone, Friends University, “Waterbird diversity at a man-made stopover wetland in an urban environment.”

Lindsey A. Walters, Northern Kentucky University, and Nathan Olszewski and Kevin Sobol, Canisius College, “Starting over: nest relocation and nestling provisioning in House Wrens after nest predation.”


Enrique Weir, The Crane Trust, “Wet meadows distribution, use by cranes and other migratory birds, and hydrological influence at South-central Nebraska: a literature and information summary and evaluation.”


Matthew Wilkins, University of Colorado, Hakan Karaardty and Ali Erdoğan, Akdeniz University, Antalya, Turkey, and Rebecca J. Safran, University of Colorado, “Geographic variation in the song of the Barn Swallow, Hirundo rustica.”


Virginia L. Winder and Steven D. Emslie, University of North Carolina Wilmington, “Ecology of Nelson’s, Seaside and Saltmarsh sparrows (Ammodramus nelsoni, A. maritimus, and A. caudacutus, respectively) and mercury availability at breeding versus non-breeding sites.”

Jared D. Wolfe, Louisiana State University, and C. John Ralph, USFS Pacific Southwest Research Station and Klamath Bird Observatory, “Gimme’ shelter: a tropical bird’s dissimilar response to
global climatic phenomenon in an uneven aged forest.”

Eric M. Wood and Anna M. Pidgeon, University of Wisconsin-Madison, “The importance of oak trees as foraging habitat for neotropical migrant songbirds during spring migration.”


Edmund Zlonis and Gerald Niemi, University of Minnesota, “Avian community dynamics in managed and unmanaged boreal forests.”

**POSTERS**


David Baasch, Platte River Recovery Implementation Program, “Platte River Recovery Implementation Program: a basin-wide approach toward recovery and ESA compliance for four listed species including Interior Least Terns and Piping Plovers.”

Jennifer Baldy, Kalamazoo Nature Center, “A method of adjusting for area overlap when using the unlimited distance method to estimate population.”

Nathan Banet, Kathleen O’Reilly, Kathleen Haan, and Dan Kim, Portland State University, “The effect of Brown-headed Cowbirds on nesting condition of hosts.”

Nyamhaya Barbary, Xiangming Xiao, John Y. Takekawa, Delong Zhao, Hongfeng Zhao, and Tseneemiyadag Natsagdorj, University of Oklahoma, “Modelling spatial distribution of Swan Goose (Anser cygnoides) in East Asia.”

Brian J. Bielfelt, Texas A&M University-Kingsville, Andrea R. Litt, Montana State University, and Fred C. Bryant, Leonard A. Brennen, and Tom Langscheid, Texas A&M University-Kingsville, “Does a native invasive grass affect breeding birds in grasslands?”

Ashley Bogrand and Diane L. H. Neudorf, Sam Houston State University, “Nest defense behavior by Carolina Wrens (Thryothorus ludovicianus) in an urban environment.”

Richard A Botta and Dale E Gawlik, Florida Atlantic University, “Effects of lake stage and marsh elevation on wading bird nesting effort at Lake Okeechobee, FL.”

Annie M. Bracey, University of Minnesota, Duluth, “Window related avian mortality on Minnesota Point, MN, USA.”

Charles R. Brown, University of Tulsa, and Valerie A. O’Brien, Oklahoma State University, “Are wild birds important in the movement of arthropod-borne viruses?”

David R. W. Bruinsma and Nicola Koper, University of Manitoba, “Does conspecific attraction explain area sensitivity of songbirds in tall-grass prairie.”


Mery Casady and Letitia M. Reichart, University of Nebraska at Kearney, and Andrew K. Birnie and Jeffrey A. French, University of Nebraska at Omaha, “Measuring fecal corticosterone in wild Whooping Cranes (Grus americana).”


Sharon Coe, Deborah Finch, and Megan Friggens, USFS Rocky Mountain Research Station, “Assessing the vulnerability of birds to climate change using a decision-support tool.”

Sheldon J. Cooper and Andrea Holzbauer, University of Wisconsin-Oshkosh, “The energetic cost of an immune challenge in Black-capped Chickadees.”

Sarah Cubaynes, Centre d’Ecoologie Fonctionnelle et Evolutive, Montpellier, France, E. A. Schreiber, Smithsonian Institution, Paul F. Doberly Jr., Colorado State University, Ralph W. Schreiber, deceased, and Olivier Gimenez, Centre d’Ecoologie Fonctionnelle et Evolutive, Montpellier, France, “To breed or not to breed: seabirds response to extreme climatic events.”

Andrew S. Dolby, D. A. O’Dell, and W. Humayon, University of Mary Washington, “Enzyme immunoassay quantification of heat shock proteins to evaluate chronic stress in birds.”

Jeff Drahoty and Letitia Reichart, University of Nebraska at Kearney, and Mark Vrtiska, Nebraska Game and Parks Commission, “Rainwater Basin wetland seed availability in annual and perennial plant communities prior to spring migration.”
Kevin Ellison and Steve Zack, Wildlife Conservation Society, "Using grassland birds to guide an ecological restoration of bison."

Dorothy A. Fatummbi and Sara R. Morris, Canisius College, "How is plumage used to determine age and sex of birds?"

Andrew Flynn and Rebecca J. Safran, University of Colorado, "Predictors of nest predation in North American Barn Swallows Hirundo rustica."

Cecily F. Foo and Timothy H. Parker, Whitman College, "Song similarity in Dickcissels (Spiza americana) is not well described by cross-correlation."

Thomas Gardali, Diana Humpie, Renée Cormier, and Nathaniel E. Seavy, PRBO Conservation Science, "Establishing the breeding provenance of a temperate-wintering sparrow with light-level geolocation."

Jessica M. Gorzo and Patrick G. R. Jodice, USGS South Carolina Cooperative Fish and Wildlife Research Unit, "Bird community distribution on golf courses in coastal Beaufort County, SC."


Jodi A. Gallicksrud and Muir D. Eaton, Drake University, "Intra- and inter-specific variations in cone photoreceptor abundances among waterfowl."

Margret I. Hatch, Penn State University-Worthington, and Robert J. Smith and T. J. Zenzal, University of Scranton, "Male and female differences in morphology including plumage coloration in a "monomorphic" species, the Gray Catbird."

Lyndon R. Hawkins and Brian D. Peer, Western Illinois University, "Egg shape and its effect on incubation temperature in the Brown-headed Cowbird."

Nicholas P. Haffeldt, Aarhus University and University of Copenhagen, Iben N. Aggerholm, Nathia H. Brandtberg, and Jacob H. Jørgensen, University of Copenhagen, and Klaus Diehm and Peter Sunde, Aarhus University, "Factors in Barn Owl (Tyto alba) natal dispersal: is it density dependence?"

William Jacek, Miranda Kiefer, Brittany Childs, and R. Given Harper, Illinois Wesleyan University, and Brian Peer, Western Illinois University, "Comparison of eggshell porosity and estimated gas flux between the Brown-headed Cowbird (Molothrus ater) and its hosts: the Dickcissel (Spiza americana) and the Red-winged Blackbird (Agelaius phoeniceus)."

Levi R. Jamison and Charles van Riper III, University of Arizona, "Rapid spread of the tamarisk leaf beetle (Diorhabda carinulata)."

Brittany Jenkins, University of Colorado, "Information content of sexual signals: a temporal investigation of stress resistance."

Erica Judd, Chris Butler, and Eric Judd, University of Central Oklahoma, "Ecological niche modeling as a method for mapping distribution of hummingbird hybrids."

Janice K. Kelly and Kenneth A. Schmidt, Texas Tech University, "Post-breeding public information use in a ground-nesting songbird community."

Mary E. Komegay and Jaime A. Collazo, USGS North Carolina Cooperative Fish and Wildlife Research Unit, Stephen J. Dinsmore, Iowa State University, and James F. Saracco, Institute of Bird Populations Point Reyes Station, "Testing assumptions underlying estimates of breeding productivity derived from mist netting data."

Eunbi Kwon and Brett K. Sandercock, Kansas State University, "Age-specific demography and population dynamics of the Western Sandpiper, Calidris mauri."

Linda A. Lait and Theresa M. Burg, University of Lethbridge, "Postglacial recolonization patterns of the Chestnut-backed Chickadee (Poecile rufescens)."

Anna Joy Lehmicke and D. B. Warnell, University of Georgia, Mark Woodrey, Mississippi State University, and Bob Cooper, University of Georgia, "Differences in breeding ecology of Seaside Sparrows in Gulf and Atlantic coastal marsh habitats."


Mia N. Malloy and Adam J. Davis, University of Georgia, “The University of Georgia Avian Biology Study Abroad Program in Costa Rica.”

Kristen Martin and Nicola Koper, University of Manitoba, “Detection of Yellow Rail, *Coturnicops noveboracensis*, using multiple-visit, call-broadcast surveys.”

David Mehlman, USFS Center for Bottomland Hardwoods Research, “Roost site of Vervain Hummingbird (*Mellisuga minima*) discovered.”


Tyler W. Moore, Hampden-Sydney College, Michael D. Collins, Rhodes College, and Adrienne J. Leppold and Rebecca L. Holberton, University of Maine, “Differential migration of passerines during spring and fall in the Gulf of Maine (USA).”

Robert K. Murphy, U.S. Fish and Wildlife Service Southwest Region, “Recent policy actions by the U.S. Fish and Wildlife Service on managing risks to and ‘take’ of eagles in renewable energy landscapes.”

Desiree L. Narango and Amanda D. Rodewald, The Ohio State University, “Variation in nestling provisioning behavior of urban and rural Northern Cardinals (*Cardinalis cardinalis*).”

Son Nguyen, Katrina Hucks, Chris Butler, and Erica Becker, University of Central Oklahoma, “The effects of temperature, light, and sugar concentration on hummingbird feeder solutions.”

Timothy Olson and John Kricher, Wheaton College, “Black-capped Chickadee (*Poecile atricapillus*) foraging behavior in mixed needle/broad-leaved forest and on a barrier beach in Massachusetts.”

Falyn Owens and Philip Stouffer, Louisiana State University, “Do site preparations in Louisiana lobolly clearcuts impact breeding disturbance-dependent birds?”

Joseph Oyugi, Wright College, “Variation in bird communities within a Brachystegia woodland: a comparative study of disturbed and undisturbed forest patches.”

Kristina L. Paxton and Frank R. Moore, University of Southern Mississippi, and Matthew D. Johnson, Humboldt State University, “Morphological, physiological, and behavioral differences characterizing two migratory populations of Swainson’s Thrushes (*Catharus ustulatus*) with distinctly different migratory journeys.”

Gary Ritchison and Tyler Rankin, Eastern Kentucky University, “Nest-site selection by Sharp-shinned Hawks in Kentucky.”

Tara Schanning, Cornell University, “Evaluating Clark’s Nutcracker, *Nucifraga columbiana*, population status, habitat use, and detectability with occupancy surveys.”

Scott W. Schmidt and Robert B. Blair, University of Minnesota, “Bird distributions across a residential-hardwood forest edge.”

Ryan Shipley, Andrea Continia, Nyambar Batbayar, Eli Bridge, and Jeff Kelly, University of Oklahoma, “Why is there a gap in the breeding range of the Painted Bunting (*Passerina ciris*)?”

Valerie Steen and Abby N. Powell, USGS Alaska Cooperative Fish and Wildlife Research Unit, and Susan Skagen, USGS Fort Collins Science Center, “Potential effects of climate change on the distribution of wetland-associated birds in the Prairie Pothole Region, USA.”

Idikko Szabo, University of British Columbia, “Bird study skin preparation website available on Beaty Biodiversity Museum website. Phase I – Complete.”


Syrena M. Taylor and Christopher M. Heck-scher, Delaware State University, “Effect of age on Veery song repertoire size.”

Jennifer L. Thieme and Amanda D. Rodewald, The Ohio State University, “Behavioral and reproductive consequences of nest predator.”

Nathan E. Thomas, Shippensburg University, and David L. Swanson, University of South Dakota, “Intraspecific correlations between minimum and maximum metabolic output in birds: do intraspecific data support the aerobic capacity model for the evolution of endothermy?”


Pepper W. Trail, USFWS National Fish and
Wildlife Forensics Laboratory, "The contemporary feather trade: exploitation of North American birds for the construction of Native American-style regalia."

Margaret A. Voss, Michael A. Campbell, and Beth A. Potter, Penn State Erie. "Using the avian nest as a model system to explore biodiversity."

Andrew Weber and Margaret Brittingham, Penn State University. "Habitat use by grassland obligate birds in south central Pennsylvania."

Walter Weltje, The Crane Trust, Felipe Chavez-Ramirez, Gulf Coast Bird Observatory, and David Brandt, Gary Krapu, and Aaron Pierce, USGS Northern Prairie Wildlife Research Center. "Using satellite telemetry to gain new insights into Whooping Crane (Grus canadensis) stopover locations and migration behavior."

Rachel Wildrick and Rebecca S. Safran, University of Colorado. "Ecological predictors of age-related increases in reproduction in Barn Swallows."*

Lauren Wilkerson and Michael Patten, University of Oklahoma. "Parental investment in the cooperative-breeding Acorn Woodpecker (Melanerpes formicivorus)."


Yufeng Zhang and David Swanson, University of South Dakota. "Metabolic rates in swallows: do energetically expensive lifestyles affect thermogenic capacities in birds?"

Hongfeng Zhao, Jinwei Dong, Youmin Chen, Delong Zhao, and Xiangming Xiao, University of Oklahoma. "Effect of climate change and urbanization on geographical range shifts of Light-vented Bulbul Pycnonotus sinensis in China."

ATTENDANCE

ALASKA: Anchorage, Margaret Petersen; Eagle River, Cecily Foo; Fairbanks, Abby Powell.


ARKANSAS: Fayetteville; Elizabeth Adam, Douglas James, Marla Steele.

CALIFORNIA: Berkeley, Jeff Whitedeker; Commerce City, Mindy Hetrick; Davis, Peter Coates; El Cerrito, Julie Jedlicka; Eureka, Sacha Heath; Fresno, Kathryn Purell; Irvine, Richard Erickson; Los Angeles, Lauren F. Tingle; Petahuna, Tom Gardali; San Diego, Barbara Kus; Santa Cruz, Kristin Ruegg; Seaside, Eric Ross; Topanga, Thomas Smith.

COLORADO: Boulder, Joanna Hubbard, Brittany Jenkins, Rebecca Safran, Matthew Wilkins; Brighton, Jennifer Blakesley, Rob Sparks; Cherry Hills, Village Rachel Wildrick; Denver, Andrew Flynn; Durango, Joseph C. Ortega; Fort Collins, Cameron Aldridge, Paul Doherty, Gabriele Engler, Kathryn Langin, Sara Oyler-McCance, David Pavlacky, Jora Rehm-Lorber, Susan Skagen, Helen Sefaier, Valerie Steen, Tammy Vercatere, Greg Wann, Reesa Yafe Conway; Golden, Levi Janison; Lafayette, Anne Bartuszewicz, Mike Carter; Lakewood, Suzanne Fellows; Las Animas, Duane Nelson; Wellington, Victoria Dreyz.

DELWARE: Dover, Kitt Heckscher, Syrena Taylor; Newark, Jeffrey Buler, Christine Rega, Greg Shriner.

DISTRICT OF COLUMBIA: Mercedes Foster, George E. Watson.

FLORIDA: Boca Raton, Tyler Beck, James Beersens, Bryan Botson, Richard Botta, Dale Gawlik, Michelle Petersen; Gainesville, Jessica Oswald; Monticello, Brad Mueller; Naples, Bette Jackson, Jerry Jackson; Pemwick, Jessica Klasse; St. Petersburg, John A. Pourtless IV; Venus, Reed Bowman; West Melbourne, Christy Pruett, Jason Smyth.

GEORGIA: Athens, Mia Malloy, Christina White; HAWAI'I: Hawai'i National Park, Steven Hess.

IDAHO: Boise, Terrell Rich; Victoria Saab; Pocatello, David Delehanty, Kristy Howe.

ILLINOIS: Bloomington, Brittany Childs, Miranda Kiefer; Champaign, Amber Alhores, Thomas Benson, Scott Chiavacci, Nicole M. Davros, Jason Fischer, Jeffrey Hoover, Matt McMinn-Louder, Kelly VanBeek; Charleston, A. Karlien Lang; Chicago, Allison Johnson, Caryn Lowther, Peter Lovicher, Dylan Maddox, Joseph Ouygi, Dai Shizuka; Minier, Butch Tetzlaff; Naperville, Anna Groves; Normal, R. Given Harper; Reynolds, Cathleen Monson; River Forest, Jennifer Mizen; Savoy, Wendy Schelsky.

INDIANA: Bristol, Doris Watt; Muncie, Kamal Islam.

IOWA: Ames, Bonnie Bowen, Stephen Dins-
more, Chris Foote, Cory Gregory, Tyler Harms, Rolf Koford, David Otis, Carol Vleck, David Vleck; Bettendorf, Brian Peer; Davenport, Walt Zuendeeg; Des Moines, Scott Anliker, Luke Campillo, Moir Eaton, Jodi Gullicksrud; Fayette, Kuta McCarville.

KANSAS: Admire, Jean H. Schuelsen; Emporia, William Jensen; Hays, Robert Channell, Victoria Cikanek, Greg Farley, Elmer J. Finck, Stephanie Kane, Scott Schmidt; Lawrence, Bryan Pahl, Peter Hosner, Carl Oliveros; Leavenworth, John Schukman; Manhattan, Gina Barton, Amy Erickson, Andrew Gregory, Lyla Hunt, Eunbi Kwon, Brett K. Sandercocck; Wichita, Chris Rogers.

KENTUCKY: Highland Heights, Lindsey Walters; Louisville, Jonathon Valente; Richmond, Gary Ritchison.

LOUISIANA: Baton Rouge, Richard Gihbons, Erik Johnson, Falyn Owens, Jared Wolfe; Bossier City, James L. Ingold.

MAINE: Gorham, Allyson Jackson; Vassie, Adrienne J. Leppold.

MARYLAND: Annapolis, Jonas Davis; Bethesda, Ellen Paul; Laurel, Jeff Spendelow; Nottingham, Bonnie Johnson, L. Scott Johnson; Tacoma Park, Terence Sillett.

MASSACHUSETTS: Brockton, Megan Shave; East Fullmouth, Betsy Davis, William E. Davis; Pocasset, John Kircher, Martha Vaughan; Sudbury, Anne Hecht.

MICHIGAN: Albion, Dale Kennedy, Doug White; Berrien Springs, Cheryl Trine; Grand Haven, Michael P. Lombardo; Kalamaezoo, Jennifer Baly, Carol Breuer, Max Breuer; Saugatuck, John Reding; Lexington, Dave Webb; Williamston, Anthony Duliso.

MINNESOTA: Duluth, Josh Bednar, Paul Dolan-Lime, Alexis Grinde, Annie McLean Bracey, Jerry Niemi, Anna Peterson; Hermantown, Ed Zlonis; Lauderdale, Erin Roche; Scandia, Todd Arnold; St. Paul, Bailey McKay, Jennifer Stucker, K. S. Gopi Sundar, Tom Will.

MISSISSIPPI: Hattiesburg, Kristen Covino, Kristina Paxton, Theodore Zenar; Leland, Paul B. Hamel; Mississippi State, Mark Woodrey.

MISSOURI: Columbia, John Faaborg, Caro Joos, Walter Welthje; St. Louis, Jerry Banet, Nathan Banet, Iris Levin, Jamie Palmer.

MONTANA: Bozeman, Kevin Ellison; Missoula, Dan Barton; Polson, Charles Blem, Leann Blem; Stockett, Harry W. Power.

NEBRASKA: Anselmo, Barbara Cooksley; Ashland, Wayne Mollhoff, Janice Mollhoff; Bennet, Terry Newby, Tom Newby; Burwell, Sarah Sortum; Central City, Greg Senkble; Denton, Marian Langen; Elba, Pete Berthelson; Grand Island, Andy Bishop, Kenny Dinan, Robert Harms, Clem Klaphake, Jeanne Lackey, Jill Liske-Clark, Timothy Smith, Brooke Stansberry; Holdrege, John Thorburn; Kearney, David Baasch, Patti Bailar, Bridget Barron, Kaitlyn Bennet, Stanley Clouse, Jeff Drahotka, Joan Dummer, Bruce Eichhorn, Sarah Focke, Thomas Freeman, Keith Geluso, Mary Harner, Alice Heckman, Roger Janosch, Jerry Kenny, Keanna Leonard, Alyx Lingenfelter, Craig Link, Elda Rogers, Kent Skaggs, D. Max Smith, Marcia Smith, Bill Taddicken; Lincoln, Craig Allen, Mary Bomberger Brown, Linda R. Brown, Todd Buckley; Zachary Cheviron, Elaine Connelly, Karie Decker, T. J. Fontaine, Robert Gibson, Bernice Goemann, Melvin Gramke, Julie Huddle, Gregg Hutchison, Karen Jensen, Paul Johnsard, Joel Jorgensen, Christopher Jorgensen, Thomas Labez, Jacki Luonis, Melissa Marinovich, Mark Mesarch, Ritch Nelson, Jeff Nothwehr, Sue Ellen Pegg, Mario Pesendorfer, Larkin Powell, John Quinn, Sarah Rehme, Dave Sands, Sergio Seipke, Ryan Stutzman, Christine Thody, Dave Titterington, Linda Titterington, Rhonda Winchell; Norfolk, Alexandra Frohberg; Omaha, Mace Hack, John McCarty; Scottsbluff, Diane Gilles, Steven Johnson, Hod Kosman; Valentine, Melvin Nenneman, Wood River, Karie Gil-Weir, Enrique Weir.

NEVADA: Reno, Christopher Briggs, Jessi Brown.

NEW HAMPSHIRE: Concord, Pam Hunt, Epsom, Rebecca Suomala.

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SOUTH AFRICA: Cape Town, Mduzzi Ndlovu.
REVIEWERS FOR VOLUME 123

Reviewers are the lifeblood of a journal as editors depend on them to help identify manuscripts with merit and offer suggestions to improve the data analysis, overall science, and writing. These individuals receive little recognition, but are extremely important in the process of improving the science and quality of what is published. We thank all of those listed below who served as referees for manuscripts processed (accepted and published, withdrawn, or rejected) after 1 July 2010 through completion (late August 2011) of the December 2011 issue of Volume 123. Those shown in boldface reviewed more than one manuscript. The Wilson Ornithological Society and the editorial staff are indebted to and thank each person who served as a reviewer.—Clait E. Braun, Editor.

Editorial News and Editor’s Comments

The Wilson Ornithological Society has selected Dr. Margaret A. Voss as the next Book Review Editor for *The Wilson Journal of Ornithology* effective immediately. Dr. Robert B. Payne earlier asked to be replaced as Book Review Editor as noted in the June 2011 Issue (124: 427) when the vacancy was announced. Applications were received from interested persons and Margaret was selected. She can be contacted at mavl1@psu.edu if you have an interest in reviewing a particular book or would like to suggest that a book be reviewed. Please note that we rarely encourage unsolicited book reviews. It was a pleasure to have Bob Payne ably serve as Book Review Editor for the last 3+ years. Some of the reviews solicited by Bob will continue to appear into 2012.

I also take this opportunity to comment on not following the taxonomic nomenclature in the 2011 Volume (123) as set forth by the Fifty-second Supplement to the American Ornithologists’ Union Check-list of North American Birds (*Auk* 128:600-613). First, my copy of the July 2011 Issue of *Auk* did not arrive until 1 August 2011. The March and June 2011 Issues of *The Wilson Journal of Ornithology* had been printed on 25 February and 1 June, respectively. The September 2011 Issue had been made up and sent to Allen Press on 1 June and was in page proofs; it was printed and released on 1 September. The December 2011 Issue was made up in mid-August and sent to Allen Press on 29 August. Thus, there was little time to again review all bird names in all of the manuscripts in the December Issue prior to sending it to the printer. Second, we have an Index under active preparation throughout the year. My view, after careful consideration, was that it would be less confusing to have all Issues of Volume 123 follow the same taxonomy for birds in North America (including Mexico) starting immediately.

Clait E. Braun, Editor
*The Wilson Journal of Ornithology*
sg-wtp@juno.com
This index includes references to genera, species, authors, and key words or terms. References are made to scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text, in addition to avian species. Nomenclature follows the AOU Check-list of North American Birds (Seventh Edition) and F. Gill and M. Wright and supplements through 2011 (Birds of the World, Recommended English Names, Princeton University Press, Princeton, New Jersey, USA and Oxford, United Kingdom). Reference is made to books reviewed and announcements as they appear in the volume.

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