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Author(s): Santiago David and Gustavo A. Londoño
Source: The Wilson Journal of Ornithology, 125(2):268-274. 2013.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/12-117.1
URL: http://www.bioone.org/doi/full/10.1676/12-117.1

The Wilson Journal of Ornithology 125(2):268–274, 2013

NESTING OF THE YELLOW-BREASTED WARBLING-ANTBIRD (*HYPOCNEMIS SUBFLAVA*) WITH NOTES ON THE NESTING BIOLOGY OF THE *HYPOCNEMIS CANTATOR* COMPLEX

SANTIAGO DAVID[1,4,5] AND GUSTAVO A. LONDOÑO[2,3]

ABSTRACT.—We provide the first detailed nesting biology information for the Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*), a member of the recently split Warbling Antbird complex. We found seven pouch-shaped nests with two eggs or nestlings within Manu National Park, SE Peru. Long incubation sessions (93.7 ± 7.78 minutes, range = 4–480 minutes, n = 18 days) were untaken by both parents and high diurnal nest attentiveness (% of time on the nest) averaged 85.8 ± 1.4% (n = 16) as a result of taking fewer short foraging trips (6.3 ± 0.6 trips/day, range = 3–11; n = 14) that lasted 16.19 ± 1.78 min (range = 1–91; n = 18). Incubation behavior produced an average inner nest temperature of 32.3 ± 0.24 °C (n = 15 days) and average egg temperature of 36.4 ± 0.09 °C (n = 3). Individual nests at different elevations exhibit differences in incubation behavior. The nestling period was 11 days (n = 1) and both parents brooded and fed the nestlings. Nest shape, location, and composition were similar to other species in the complex, but egg coloration was variable among species. *Received 9 July 2012. Accepted 26 January 2013.*

Key words: breeding biology, eggs, *Hypocnemis subflava*, incubation behavior, nest, Warbling-Antbird.

The Warbling Antbird (*Hypocnemis cantator*) was considered a widespread polytypic species (Zimmer and Isler 2003), but recently it has been split into six different species based on genetic, vocal, and plumage coloration differences among populations (Bates et al. 1999, Isler et al. 2007). One of these species is the Yellow-breasted Warbling-Antbird (*H. subflava*), distributed from central Peru to central Bolivia and western Brazil. It occurs in sympatry with the Peruvian Warbling-Antbird (*H. peruviana*) in part of its range (Isler et al. 2007, Tobias and Seddon 2009). Two subspecies were maintained by Isler et al. (2007), *H. s. subflava* and *H. s. collinsi*, with the first one restricted to the Andean foothills in east central Peru (Zimmer and Isler 2003).

Antbird breeding information and nest descriptions have increased in recent years, providing not only new natural history data but also insight into the family's phylogenetic history (Zimmer and Isler 2003). Nest architecture and nesting behavior can be useful for avian systematics (Sheldon and Winkler 1999), and this evidence could be important for understanding geographic variation and species-level taxonomy in complex groups within Thamnophilidae (e.g., Isler et al. 2006).

Nest and egg descriptions have been published for some populations of the *H. cantator* complex, specifically from N Brazil (n = 1), Guianan region (n = 3), Colombia (n = 1) and SE Peru (n = 1) (Hellebrekers 1942, Oniki and Willis 1982, Tostain et al. 1992, Haverschmidt and Mees 1994, Cadena et al. 2000, P. Marra cited in Zimmer and Isler 2003). Of these, only one could be assigned as *H. subflava*. Zimmer and Isler (2003) reported limited nesting information for the genus *Hypocnemis*; it is known that both parents incubate during the day for a period of at least 12 days and a nestling period of 11 days had been reported in the complex. Detailed information on the nesting biology for the species in the *H. cantator* complex is lacking. Our objective is to provide the first detailed description of the nest, eggs, nestlings, incubation behavior, and nest microclimate for the Yellow-breasted Warbling-Antbird and revise nesting biology knowledge in the genus *Hypocnemis*.

METHODS

Study Area.—We studied the Yellow-breasted Warbling-Antbird (*H. subflava*) during three consecutive breeding seasons, from August–December in 2008–2010 at two stations in Manu National Park, Cusco, Perú. The stations were located on the Andean foothills adjacent to Tono (12° 57′ 24.6 ″ S, 71° 33′ 51″ W) and San Pedro (13° 03′ 19.4″ S, 71° 32′ 48.5″ W) rivers, and we made observations between 840–1,450 m asl. The

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[1] Instituto de Biología, Universidad de Antioquia, A.A.1226, Medellin, Colombia.

[2] Florida Museum of Natural History, Dickinson Hall, University of Florida, Gainesville, FL 32611, USA.

[3] Department of Biology, 227 Bartram Hall, University of Florida, P. O. Box 118525, Gainesville, FL 32611, USA.

[4] Current Address: Biodiversity Research Centre and Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

[5] Corresponding author; e-mail: sdavid@zoology.ubc.ca

area comprised premontane forest with a canopy height of up to 40 m and montane cloud forest with extensive stands of bamboo (*Guadua* spp.).

Nest, Egg, and Nestling Measurements and Provisioning Behavior.—Calipers with an accuracy of 0.1 mm were used to measure nest and egg dimensions. Egg weights were collected with a digital scale with an accuracy of 0.05 g (Flip-Scale F2, Phoenix, AZ, USA, www.myweigh.com). Tarsus length and wing chord of nestlings were measured using a ruler to the nearest 1 mm. A motion sensor-triggered camera (PC85 Rapidfire professional; Reconyx Inc., Holmen, WI, USA) was placed 0.7 m from the nest and camouflaged with vegetation to avoid interference with parental behavior. The camera was programmed to take 10 photographs with any movement on the nest, which allowed us to record provisioning behavior during nestling period. All means are reported with their standard error (SE).

Incubation Rhythm and Nest Microclimate.—Thermal sensors were used to monitor nest microclimate and incubation behavior in three nests. Two sensors were placed in two nests that had developed eggs; one sensor was located at the bottom of the nest under the eggs, and the second was attached to the exterior side of the nest wall. These sensors collected inner and outer nest microclimate, respectively. Incubation behavior was monitored for seven and eight days at each of the nests respectively, and the last six days of incubation were used for comparisons between different elevations. An extra intra-egg sensor was placed in a third nest that contained two fresh eggs. The thermal sensor was inserted into the egg through a small hole made in the large end and was sealed with super glue (Londoño 2009). This nest was depredated and data collection was only possible for 3 days. Sensors were connected to a U-12 HOBO data-logger (Onset Computer Corporation, Pocasset, MA, USA, www.onsetcomp.com) that recorded temperatures every minute until the eggs hatched or predation occurred. We used these data to estimate parental nest attentiveness (percentage of time on nest during incubation period) and incubation behavior (i.e., number and duration of trips), which are calculated through temperature fluctuations (Cooper and Miles 2005, Londoño 2009). We checked these data for normality and compared incubation behavior between two nests located at different elevations using a *t*-test.

RESULTS

Nest Descriptions and Sites.—Most Yellow-breasted Warbling-Antbird nests were found at elevations below 1,000 m asl. The highest nest was located at 1,300 ± 7 m asl in the San Pedro station. We found seven nests located in dense understory areas near small streams placed in dense vegetation with abundant shrubs, ferns, and vine tangles. All of these nests were deep and pouch-shaped mostly woven to branch forks of seedlings and were suspended from the nest rim on average 0.86 m (range = 0.3–1.8 m; $n = 6$) above ground (Fig. 1A). Nests had two distinctive layers that together weighed 11.8 ± 0.8 g ($n = 5$). The external layer weighed 10.7 ± 0.8 g ($n = 5$) and was composed of large dried bamboo (*Guadua* spp.) leaves (80%), green moss (10%), and decomposing palms and trees leaves (5%), all of which were woven with dark rhizomorphs and rootlets (5%). The lining, made of dry grass fibers (50%) and dark rootlets (50%), weighed 1.0 ± 0.2 g ($n = 5$).

The inner diameters of the cup were 53.5 ± 2.68 mm by 46.65 ± 3.24 mm ($n = 6$). The wall thickness and cup depth were 14.73 ± 2.63 mm and 52.91 ± 2.64 mm ($n = 6$) respectively, and the outer dimensions of the nest were 78.93 ± 5.44 mm by 74.51 ± 3.46 mm and 89.38 ± 4.29 mm ($n = 6$) high.

Clutch Size and Eggs.—All nests had two eggs or nestlings ($n = 7$). The second egg was laid two days after the first egg was laid ($n = 3$). Eggs were white with dark maroon spots and streaks; however, the dark maroon markings varied among individuals. Eggs in some clutches were white with few and small scattered dark maroon spots, and in others, eggs were white with a dense network of dark maroon streaks and spots covering the entire surface of the egg (Fig. 1B). Eggs measured 20.2 ± 0.26 by 14.2 ± 0.19 mm and weighed 2.1 ± 0.1 g ($n = 12$).

Incubation.—Both adults were observed attending the nest ($n = 5$) during the day through opportunistic videotape and camera trap photographs. The incubation period could not be determined because of predation in four nests with fresh eggs. We monitored incubation behavior for 414.9 hrs in three nests with sensors (191, 177.9 and 46 hrs, respectively); the eggs were incubated during 380.6 hrs (91.7% of the time). High diurnal nest attentiveness (85.8 ± 1.4%; $n = 16$ days) resulted from long incubation periods

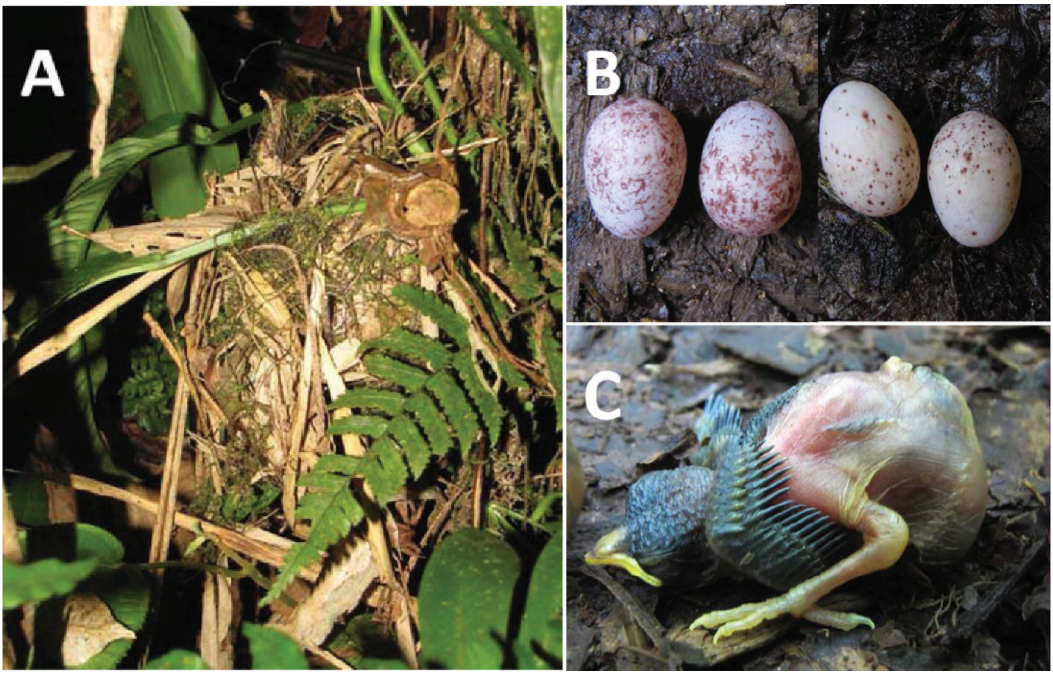

FIG. 1. Nest, eggs, and nestling of the Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*) in Manu National Park. A) Lateral view of a nest located at 956 m asl, B) Egg marking variation among individuals and C) Five day old nestling.

and a few short foraging trips. The parents averaged 6.3 ± 0.6 (foraging trips/day range = 3–11; $n = 14$) that lasted 16.19 ± 1.78 (range = 1–91 min; $n = 18$). In contrast, the incubation bouts were longer 93.7 ± 7.78 (range = 4–480 min; $n = 18$). On three occasions, the female incubated most of the afternoon and through the night, generating a long incubation event between 15 and 16 continuous hours.

Inner nest temperature averaged 32.3 ± 0.24 °C ($n = 15$ days) when the adult was incubating, decreasing to 26.0 ± 0.29 °C ($n = 15$) during incubation recesses. Egg temperature was higher 36.4 ± 0.09 °C ($n = 3$) when the adult was incubating and decreased to 27.5 ± 0.65 °C ($n = 3$) during incubation recesses.

Individual nests at different elevations exhibited statistically significant differences in incubation behavior during the last 6 days of incubation. In a nest in the San Pedro station at 1,312 m asl, diurnal nest attentiveness was on average higher (90.47 ± 2.48%) compared to a nest in the Tono station at 956 m asl (83.89 ± 1.47%) (Fig. 2C; $t_{10} = 2.28$, $P = 0.046$). However, these differences were not reflected in the inner nest temperature when an adult was incubating. Despite longer time on the nest, the nest temperature for the San Pedro nest was significantly lower (30.89 ± 0.60 °C) compared to the Tono nest (34.78 ± 0.46 °C) (Fig. 2A; $t_{10} = 5.08$, $P < 0.001$). The external sensor recorded similar ambient temperature fluctuations in both nests. In the San Pedro nest, the ambient temperature was between 16 and 25.2 °C, while in the Tono nest, temperature fluctuated between 15.7 and 24 °C. Total number and duration of foraging trips also differed between nests at different elevations ($t_{10} = 3.16$, $P = 0.010$ and $t_{10} = 4.55$, $P = 0.001$ respectively). The San Pedro pair made 8.2 ± 1.0 foraging trips/day that lasted 9.0 ± 2.1 mins; in contrast the Tono pair made fewer foraging trips per day (4.5 ± 0.6), which lasted longer (26.8 ± 3.3 min) (Fig. 2B, D).

Nestling Period.—Two nests with nestlings were depredated during first day after hatching; however, in one nest we were able to identify the exact hatching and fledging days, leading to a nestling period of 11 days. The one-day-old nestlings weighed 2.3 ± 0.2 g. These chicks had pinkish skin that was completely naked. Their feet

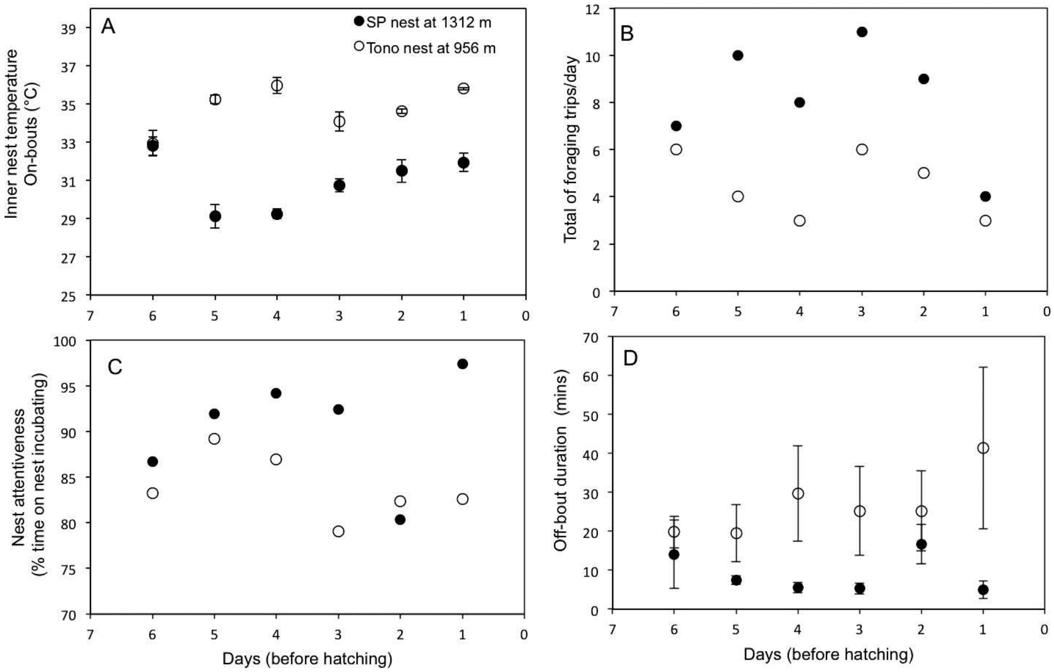

FIG. 2. Comparison of incubation behavior between two nests of *Hypocnemis subflava* located at different elevations. (A) Inner nest temperature during incubation, (B) total number of foraging trips per day, (C) daily percentage of nest attentiveness, and (D) average daily duration of foraging trips. Bars represent standard errors of the mean. Day 0 represents the hatching day for both nests. The San Pedro nest (solid circles) was found at 1312 m elevation and the Tono nest (open circles) at 956 m elevation.

and gapes were yellow, and the upper bill was gray. The tarsus and wing measured 8.0 and 7.0 ± 1.0 mm, respectively. The six-day-old nestlings weighed 8.7 ± 0.2 g and their eyes were slightly open. They had gray pin feathers on their head, back, flanks, breast, and wings, and yellow pin feathers on their wing coverts and belly. Their tarsus and wing measurements were 17.5 and 22 ± 1.0 mm, respectively (Fig. 1C). On day 11, their tarsus measured 22 mm and their wings were 40.5 mm long, and they weighed 11.8 ± 0.5 g. At this point the eyes of the nestlings were completely open and their bodies were covered with well-developed feathers, which included two distinct yellow wing bars.

Feeding behavior was documented in one nest where both adults were observed brooding and provisioning chicks, but although these are sexually dimorphic, parental investment by each sex could not be determined with the photographs. Adults provisioned the nestlings at an average of 2.03 ± 0.16 trips/hr ($n = 35$ hrs) early in the nestling period (days 1–3), increasing to 4.79 ± 0.95 trips/hr ($n = 20$ hrs; days 4–5) and 7.19 ± 0.38 trips/hr ($n = 22$ hrs) in the last stage of nestling development (days 9–11). Feeding items observed from photographs were butterflies, crickets, caterpillars, beetles and spiders.

DISCUSSION

The two-egg clutch size and the biparental care in *H. subflava* are consistent with previous reports for the Thamnophilidae (Skutch 1996, Zimmer and Isler 2003). Similarly, taking two days to lay a second egg is widespread among species in this family (Skutch 1996, Zimmer and Isler 2003). Nest attentiveness (85% of time on the nest) during incubation in *H. subflava* is high compared to other Neotropical passerines (Tieleman et al. 2004, Auer et al. 2007), but such high attentiveness is expected for species with shared incubation (Martin et al. 2007). The high percentage of diurnal incubation >82%, long incubation sessions of >100 mins, and an average egg temperature around 36 °C in *H. subflava* have also been observed in open-cup nesters of the family Thamnophilidae in Central and South America (Willis and Oniki 1972, Skutch 1996, Sheldon and

TABLE 1. Egg descriptions in the *Hypocnemis cantator* complex assigned to currently recognized species and subspecies according to Isler et al. (2007) and Remsen et al. (2012).

Taxon	Location	Egg description	Reference
H. cantator notaea	French Guiana	rosy-white covered with fine rose network, darker and more spotted at larger end	Tostain et al. 1992
H. cantator cantator	Suriname	pinkish-white with small purplish-grey markings and few larger purplish spots	Hellebrekers 1942
	Suriname	creamy-white sparsely spotted chocolate-brown	Haverschmidt and Mees 1994
H. cantator cantator	N Brazil	white with brown spots	Oniki and Willis 1982
H. flavescens[a]	Colombia	pinkish with purple streaks and spots, mostly on the large end	Cadena et al. 2000
H. subflava collinsi	SE Peru	white with brownish-red specks and streaks	P. Marra cited in Zimmer and Isler 2003

[a] *H. flavescens* presumably would be the species present in this region (C. D. Cadena, pers. comm.)

Greeney 2008, Tieleman et al. 2004). Likewise, exceptional parental investment with long sessions of incubation >15 hrs have been reported in another antbird species, *Thamnophilus punctatus* (Oniki 1975).

Incubation behavior varied between two nests at different elevations. This may have resulted from differences in energetic requirements generated by ecological pressures associated with elevation (e.g., predation risk, food availability), but the lack of ambient temperature variation between the two elevations suggests that temperature may play a minor role on the observed differences in nesting behavior. Nest predation has been identified as the main cause of nesting failures for tropical birds (Skutch 1985) and particularly cup-nesters (Oniki 1979). Six of the seven nests in our study were depredated, which corresponds to 85.7% of nests found; low nesting success has been observed in the Tono station (Valdez-Juarez and Londoño 2011, GAL, unpubl. data) and higher success in the San Pedro station (GAL, unpubl. data). These differences in nest predation could be responsible for the observed behavioral differences (e.g., reduction in the number of trips to the nest during incubation in the Tono station nest), which have been linked to high nest predation pressure (Ghalambor and Martin 2002).

A nestling period reported for nine open-cup nesting passerines with biparental care in South America averaged 14.1 days (Auer et al. 2007). The 11-day nestling period of *H. subflava* is three days shorter compared to this average; however, short nestling periods are common among open-cup nesting antbirds (8–13 days; Skutch 1996). Nestling feeding rates increased with age of the nestlings up to 7.19 trips/hr in the last stage of nestling period; in antbirds the average hourly feeding rate per nestling is often up to three times lower (Skutch 1996) compared to our study. The nestling mass before leaving the nest (11.75 g) was 2 g lower than adult mass collected in the study area for *H. subflava* (13.8 g, $n = 3$) (J. Jankowski, unpubl. data).

The nesting season of the Yellow-breasted Warbling-Antbird in our study site (Aug–Nov) occurs at the beginning of the rainy season in the area and differs from the temporal season reported for other species of the *H. cantator* complex (May–Oct in Suriname, Mar and Jul–Nov in French Guiana, Apr–Dec in Ecuador, Jul–Aug in Brazil; Zimmer and Isler 2003), but it is similar to the breeding activity reported for *H. subflava* and *H. peruviana* in SE Peru (Tobias et al. 2011). Nest shape, placement, height, microhabitat, and composition are consistent with those reported for other populations of the *H. cantator* complex in different areas (Oniki and Willis 1982, Tostain et al. 1992, Cadena et al. 2000); although, a nest reported in SE Peru presumably of subspecies *H. s. collinsi*, was described as cup-shaped (P. Marra cited in Zimmer and Isler 2003) and a subsequent review described the nest as a pouch with architecture and dimensions similar to other members of the group (M. Isler, pers. comm.). Egg coloration varies among species in the *Hypocnemis* complex (Table 1); these egg coloration differences among *Hypocnemis* species seem to support the already recognized evolutionary differences among populations based on their plumage coloration, vocalizations, and genetic structure (Bates et al. 1999, Isler et al. 2007). However, variations in egg markings within the same population remain unexplained and require further study.

Hypocnemis subflava is the only Warbling-Antbird in our lower montane study area, and this has been validated through capture and point count data (J. Jankowski, pers. comm.). However, in lowland forests at 300 m asl within the same region and in another locations, *H. subflava* and *H. peruviana* co-occur in sympatry, sometimes at high population densities. In these areas they partially segregate by habitat, with *H. subflava* occurring mainly in patches of *Guadua* bamboo and *H. peruviana* in terra firme forest (Isler et al. 2007, Tobias and Seddon 2009, Tobias et al. 2011). In our site, we found nests of *H. subflava* in bamboo and dense understory vegetation outside bamboo, suggesting that *H. subflava* can use other nesting habitats beside *Guadua* bamboo when *H. peruviana* is absent. Detailed reproductive biology and nesting site competition studies on these species when they co-occur could elucidate habitat specificity and requirements, and could also provide information to better understand their spatial segregation.

Our data for the Yellow-breasted Warbling-Antbird reveal incubation with relatively high biparental investment and a short nestling period. Most antbird breeding information has been generated in Central America (Skutch 1996, Zimmer and Isler 2003). However, we know much less about antbird nesting strategies in the Amazon, a region with the highest diversity of antbird species (Ridgely and Tudor 1994, Stotz et al. 1996). Considering this level of species diversity, compiling information about Amazonian antbird reproductive strategies is an important component for understanding why Thamnophilidae species have been so successful in the region. Detailed descriptions and quantitative natural history information is critical to understanding broader patterns and testing of hypotheses of ecological or evolutionary significance (Greeney et al. 2008). Breeding biology information for many antbirds, as well as in other tropical bird species, is sparse or lacking; it is crucial to compensate the historical bias of natural history information towards temperate species (Martin 1996) in understanding avian life history variations.

ACKNOWLEDGMENTS

We are especially grateful to Manuel Sánchez and Sebastian Pérez for valuable help in the field, and Jill Jankowski for sharing unpublished data with us. We thank Jessica Oswald, Jill E. Jankowski, M. Isler, M. Bomberger Brown, and an anonymous referee for suggestions and corrections that improved this manuscript. Our study was possible thanks to the logistical support of the NGO Peru Verde that allowed use of the Cock of the Rock Reserve during 4 years and the SERNAP that allows us to work in the Manu National Park. Financial support was provided by the Dexter Fellowships in Tropical Conservation Biology, Alexander Skutch Award (Association of Field Ornithologists), Louis Agassiz Fuertes Award (Wilson Ornithological Society), and Alexander Wetmore Award (American Ornithologists' Union).

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