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INCUBATION BEHAVIOR OF THE PERUVIAN ANTPITTA (*GRALLARICULA PERUVIANA*)

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Comportamiento de incubación del Gralarita Peruana (*Grallaricula peruviana*).

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While the nests of half of the eight species of *Grallaricula* antpittas have been described (Schwartz 1957, Holley *et al.* 2001, Greeney *et al.* 2004b, Greeney & Sornoza 2005), there are few quantitative data available for adult behaviors at the nest. Both sexes are known to incubate in Slate-crowned (*G. nana*) and Peruvian (*G. peruviana*) antpittas, and in the Peruvian Antpitta both participate in all aspects of nesting (Greeney *et al.* 2004a, 2004b, Greeney & Sornoza 2005). A covert approach to the nest by adults has been observed for Ochre-breasted (*G. flavirostris*) and Peruvian (Maillard & Vogle 2003, Greeney *et al.* 2004b) antpittas, but little else is known about general breeding behavior or incubation rhythms in particular.

Here I present the results of over 110 h of observation during incubation at a nest of the Peruvian Antpitta, from the day after laying the single egg (26 April 2003) to the day before it hatched (14 May). This was the same nest, which had an incubation period of 20 days, previously reported from northeastern Ecuador (Greeney *et al.* 2004a) near the Yanayacu Biological Station and Center for Creative Studies (00°35.95S, 77°53.40W). The shallow mossy cup nest was videotaped, from a tripod placed 5 m away, from 05:45 h to 18:15 h (EST) on the 1st through 5th day of incubation, and again on the 14th, 15th, 17th, and 19th day of incubation. Adults were sexed using the plumage differences outlined by Greeney *et al.* (2004b). Patterns of attendance by adults are presented for the period from 06:00 to 18:00 h (roughly daylight hours in the area). Due to poor quality video I was unable to observe detailed behaviors at the nest for most of the observation period., but was able to correct video problems to quantify detailed behaviors for a small portion of the observation period. In total, usually in small 5–10 minute segments, I was able to carefully transcribe 32.6 min of incubation time for the female and for 94.5 min of incubation time for the male. Means are presented with ± SD.

Behaviors at the nest. The following data are based on a total of 127.1 min of video during which the quality was sufficient to observe detailed behaviors. Numbers presented for "adults" were generated using this subsection of video, while data refering to a particular sex uses only the high-quality video available for that individual (see above). While incubating, both adults frequently (12.7 times per h) stood and peered at the nest and egg. The male did this more freqently (15.2 times per h) than the female (5.6 times per h). After standing, adults engaged in one of several behaviors. I observed both adults engage in rapid and sharp probing maneuvers. These are swift movements of the bill directed towards the lining of the nest and hypothesized to be forms of parasite removal in other birds (Haftorn 1994, Greeney 2004). In some instances, rapid probing appeared to facilitate rolling of the egg, but I never observed either sex deliberately roll the egg. I observed rapid probing behavior on 48% (13/27) of standing bouts, and both adults together probed an average of 0.59 times per bout. The female rapid-probed on 2/3 (67%) standing bouts and the male on 11/24 (46%). Apart from this the male spent 0.8% of his time preening in 10 periods averaging 4.2 ± 4.6 s (range = 1–17 s). The female spent only 2 s preening in two periods of 1 s (0.1% of her time). Both adults occasionally arranged stray rootlets and were occasionally seen to yawn or to close their eyes for a few seconds (< 30 s.), but spent the majority of their time sitting relatively still and peering about with sharp movements of their heads. Totaling these behaviors for both sexes during 2.1 h of quantified incubation, adults spent 2.8% of their time on the nest moving about, with the female spending only 1.2% of her time and the male 3.3% of his time.

On several occasions during the entire observation period (110 h), the male (20 times) or the female (10 times) arrived at the nest with a single rootlet or, less frequently, with a small clump of moss which they dropped into the nest and arranged before settling onto the egg. Adults brought nest material mostly during the first 4 days, but the male brought a rootlet to the nest the day before hatching. Both sexes also engaged in a behavior which I have rarely observed at the nests of other passerines. While incubating, they would occasionally peer intently in a single direction for several seconds and then leap off the nest in that direction. They always returned to the nest within a minute, often rapidly opening and closing their bill slighly as if having just ingested something. I believe adults were hunting for and capturing prey while incubating. I saw each adult do this 18 times during 110 h of observation.

On the first day of incubation, the female arrived at the nest with a small insect prey item in her bill. After a few seconds she ate the insect. On the second day of incubation, when the female arrived at the nest to relieve the male for the last time that day, she brought with her a small insect (< 5 mm), which she fed to the male before he left. I observed the male bringing food to the nest on day 14. Like the female, he peered around then ate the prey item after a few seconds. On the 19th day of incubation, the female stood suddenly from the incubating position, peered into the egg cup, and probed rapidly with her bill as described above. Her sudden movement pushed the egg from under her, leaving it on the mossy rim of the nest behind her. Upon settling she appeared restless and soon turned around and discovered the egg. She sat back down and peered at the egg, pecking it gently 5–6 times before remaining in the incubating position, facing the egg, for over 20 min. Each time she pecked the egg, it moved closer to falling, and when she flushed

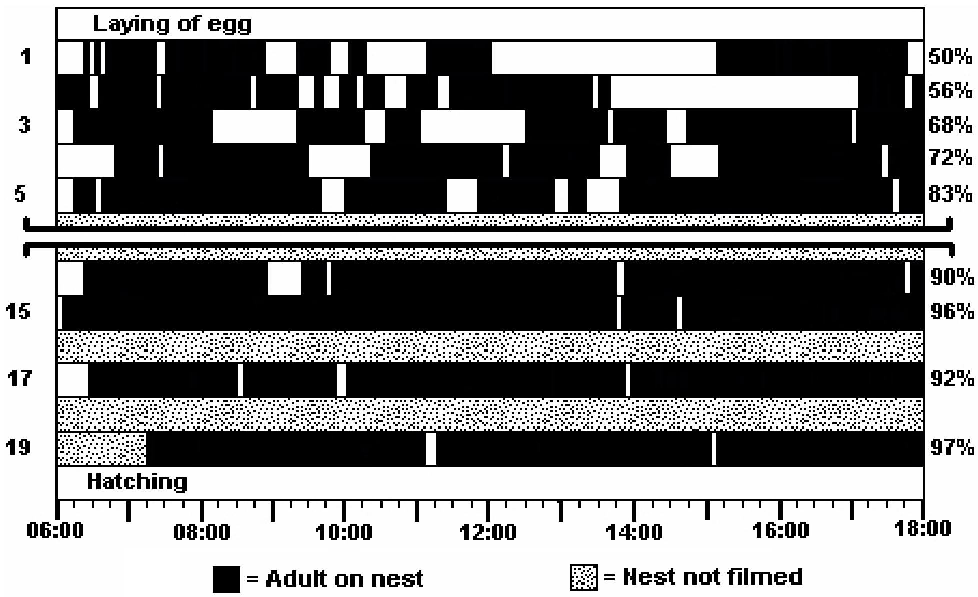

FIG. 1. Nest attendance by both sexes of the Peruvian Antpitta during incubation. On-bouts are represented by black, off-bouts by white, and periods without observations by stippled areas. Numbers on left refer to the day of incubation (after laying of the egg) and numbers on the right represent total percent coverage of the egg for the day. Time of day (24 h clock) is shown below. Periods of absence <1.5 min are not shown.

from the nest at my arrival 20 min later, the egg nearly fell. I replaced the egg and she returned shortly to continue incubating. I feel certain, had I not intervened, the egg would have fallen from the nest upon the next arrival of an adult. On at least five occasions, I observed the female calling from the nest for periods of up to 5 min. She made only the single note call previously described for this species (Greeney *et al.* 2004b), twice upon arrival at the nest and continuing for several minutes, and for three brief periods while incubating.

General patterns of attendance. In only three instances, when adults switched places at the nest, were both adults present on the nest simultaneously. Usually one would leave and the second would arrive 30–90 s later. Irrespective of the reason for leaving the nest, periods of incubation by both adults ranged from less than a minute to 3 h, but were frequently interrupted by adults chasing after prey. For the entire period, 167 visits to the nest averaged (± SD) 29 ± 30 min, but if brief departures to capture food are omitted, periods of attendance averaged 37 ± 34 min. If, in addition, periods of less than 1.5 min during changeovers are omitted, periods of attendance (both sexes combined) averaged 66 ± 61 min. During the first two days of incubation, coverage of the egg was only around 50% of daylight hours. This increased to around 80% on day six, and remained over 90% after day 14 (Fig. 1). Coverage of the egg for the entire observation period was 78%.

Participation of the sexes. At the beginning of each filming period, the female was observed to have spent the night on the nest. She generally left the nest before full daylight, usually

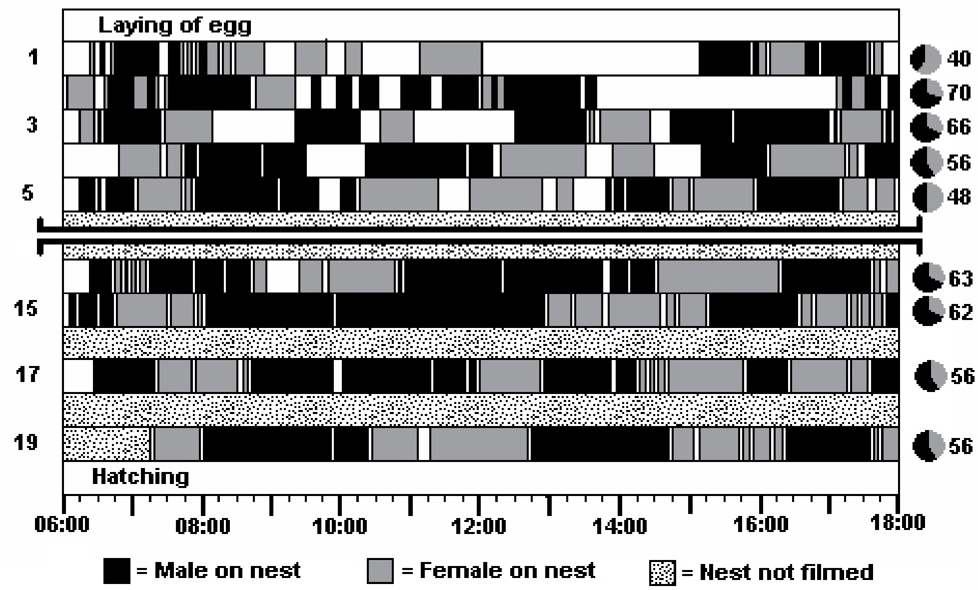

FIG. 2. Patterns of nest attendance of the Peruvian Antpitta showing the relative roles of each sex during incubation. On-bouts by the male are represented by black, those of the female by grey, and periods without observations by stippled areas. Numbers on left refer to the day of incubation. Numbers and pie charts on right show the percentage of each day's incubation duties performed by the male. Time of day is shown below. All periods of absence, including brief switches at the nest are shown.

between 05:30 and 05:50 h, and returned to the nest after dark between 18:15 and 18:30 h. On days 1–4, the female returned after 06:00 h to perform the first period of attendance, but on subsequent days the male was the first to arrive. On the first day of incubation, the female spent the majority of time on the nest and, on the second day, the male spent more time. After this, however, incubation duties were shared, with the male usually spending slightly more time at the nest (Fig. 2). For the entire observation period, the male performed 58% of incubation. The male visited the nest 78 times for periods averaging 36 ± 36 min covering the egg. The female visited the nest 89 times for periods of 23 ± 23 min. If brief periods to capture prey are omitted the male's periods of attendance averaged 45 ± 40 min and the female's were 29 ± 25 min.

Mass-loss of the egg. I weighed the egg the day after laying, recording the time to the nearest 15 min, and the weight to the nearest 0.001 g. To insure accuracy, the egg was placed on the balance three separate times at each weighing, and the results averaged. To allow for uneveness of the scale, a standard weight was measured and raw egg weights adjusted with this value. I subsequently weighed the egg on days 8, 13, and 17 of incubation (Fig. 3). From day 1 to day 17 of incubation the egg lost mass at a rate of 0.031 g/day or 0.9% of its mass/day. Using my observed rates of mass-loss, I estimate a fresh-egg-weight of 3.58 g and an overall loss of 18% of its mass during 20 days of incubation.

Conclusions. Like other Formicariidae, the Peruvian Antpitta shows a high percentage of egg coverage during daylight hours, especially

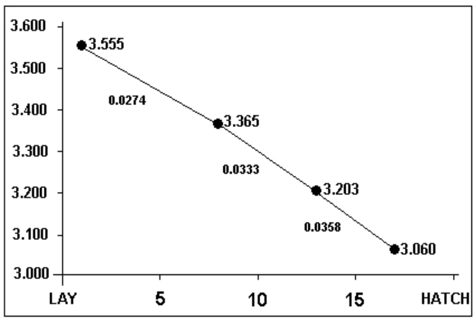

FIG. 3. Mass-loss of an egg of the Peruvian Antpitta during incubation. Numbers on the line represent absolute weight of the egg (g) and numbers below the line show rates of mass-loss between weighings (g/day).

in the last part of incubation (Skutch 1996, Dobbs *et al.* 2001, Price 2003). Combining the behaviors at the nest of both sexes, the Peruvian Antpitta showed very similar activity patterns to its congener, Slate-crowned Antpitta (Greeney & Sornoza 2005). To date, Peruvian Antpitta is the sixth antpitta that has been observed engaging in rapid probing at the nest (Dobbs *et al.* 2003, Greeney & Sornoza 2005, Greeney & Gelis 2005, Martin & Greeney 2006, Greeney & Martin 2005). This suggests rapid probing is a wide-spread behavior within the family and we encourage others to quantify observations with the goal of understanding its role in parasite removal, nest cleaning, and egg rolling (e.g., Haftorn 1994). Other antpittas have also been observed vocalizing at or near the nest (Skutch 1969, Dobbs *et al.* 2003, Kofoed & Auer 2004, Greeney & Martin 2005), but the purpose and frequency of such communication remain poorly understood. The egg of Peruvian Antpitta showed slightly higher total percent mass-loss when compared to Scaled Antpitta (*Grallaria guatimalensis*) (Dobbs *et al.* 2003), and considerably higher loss than that observed in Chestnut-crowned Antpitta (*G. ruficapilla*) (Martin & Greeney 2006). Until reported sample sizes increase for this and other species, however, it remains difficult to speculate on the causes of such variability. Undoubtedly, the interaction of rates of mass-loss (i.e., water-loss) from the egg, microhabitat selection, incubation constancy, development rates, and other factors play an important (but unexplored) role in the breeding biology of these and other tropical passerines (Ar & Rahn 1978, 1980; Ar 1991). I encourage others to gather and report information on this, and other aspects, of the biology of these fascinating and increasingly threatened Neotropical birds.

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