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Notes on egg laying, incubation and nestling care in Scaled Antpitta *Grallaria guatimalensis*

Robert C. Dobbs, Paul R. Martin, Chelina Batista, Hannah Montag and Harold F. Greeney

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En base a observaciones hechas en seis nidos de *Grallaria guatimalensis regulus* en Loja, Ecuador en 2001, describimos la asistencia al nido y comportamiento de los adultos durante los períodos de puesta de huevos, incubación y atención de los pichones. Luego de una asistencia al nido limitada e irregular durante la puesta, documentamos un período de incubación de 17 días en el cual los adultos fueron observados incubar hasta el 96% de las horas de luz. Los adultos pasaron el 83% de su tiempo criando pichones de menos de un día de edad, pero sólo el 23,3% del tiempo criando pichones de 10–12 días de edad. La frecuencia de visitas de alimentación por los adultos se incrementó de 1,09 a 2,96 comidas/hora a medida que los pichones crecieron de menos de un día a 10–12 días de edad.

Introduction

Scaled Antpitta *Grallaria guatimalensis* occurs from central Mexico to central Bolivia and spends most time on or near the ground, primarily in montane evergreen forest in the upper tropical zone (900–1,600 m)[3,5]. Like most Formicariidae, which tend to skulk secretively in heavily shaded and often dense understorey, its nesting habits and behaviour are poorly known. Much of our knowledge of *G. guatimalensis* breeding biology is based on a *G. g. regulus* population in south-west Ecuador which builds large, bulky cup nests, 0.6–1.3 m above ground, typically in a fork or crotch of an upright tree trunk, and less frequently in a tangle of smaller branches[1]. Females usually lay two unmarked turquoise eggs, incubated by both parents. Adults feed and tend the young in the nest for 17–19 days[1].

Here we supplement the only published descriptions of *G. guatimalensis* nest attendance and parental care[1] with additional information from the same population. We also describe other behavioural details of egg-laying, incubation and nestling care, and document the duration of the incubation period.

Study area and methods

Observations were made on 23 February–31 March 2001 at six nests within montane evergreen forest, at 2,000–2,100 m elevation, 10 km west of Celica (04°07'S 79°58'W), Loja province, Ecuador. The forest was characterised by heavy epiphytic (especially moss) growth and a canopy of c.25 m in height. Field observations were made in a series of relatively undisturbed tracts of forest, bordered by pasture or second growth, and connected by narrow forest corridors.

Nests were videotaped during egg-laying, incubation and nestling stages for periods ranging from 6.23 to 11.9 hours. Video cameras not mounted on tripods were placed on the ground, as close as 3 m from a nest, and concealed with leaves; cameras mounted on tripods were placed farther (10–15 m) from nests to avoid affecting the birds' behaviour. Birds did not appear to be affected by the presence of the cameras. Videotapes were transcribed at a later date.

Results

Egg laying and incubation

One nest, found during construction, was monitored closely throughout egg laying. This nest appeared complete, with the cup lined, on 5 March. One egg was laid between 17h05–17h15 on 7 March; a second egg was laid between 13h00–18h00 on 9 March. During the 44–48 hours that elapsed between laying events, limited and irregular incubation behaviour commenced. On 8 March, adults did not visit the nest between 06h50 to 18h00. The first visit to the nest was at 18h01, when one adult visited the nest, rearranged the nest material slightly, and incubated the egg until 18h34 (4.5% of the 11.9-hour observation). On 9 March, the egg was incubated 23% (86 minutes) of a 6.23-hour observation (06h30–13h00), during two separate bouts lasting 28 and 58 minutes. Adults were not present at the nest and the eggs were cool to the touch during periodic monitoring on 10–11 March. Regular incubation commenced on 12 March and both eggs hatched on 29 March after 13h00, i.e. a 17-day incubation period, although 22 days elapsed between the presence of the first egg and both eggs hatching. These eggs, which were measured immediately before (10 March) and after (15 March) incubation commenced and just prior to hatching (28 March), showed similar patterns of water loss over the incubation period, decreasing in mass by 15.5–17.0% from their original mass (Table 1).

A different nest was observed between 06h54 and 18h40 on 27 February, which was during the first five days of incubation. Both adults incubated the two-egg clutch for 96% (676 minutes) of the

11.76-hour observation. The mean (± SD) duration of six separate incubation bouts was 112.7 ± 53.9 minutes (range: 14–174 minutes). Typically, the incubating adult departed the nest immediately before its mate arrived, with time intervals between bouts ranging only 0–2 minutes. Both adults were present at the nest on only one of five exchanges, during which one adult arrived at the nest with food. The other adult, however, flew from the nest without the food, and the arriving individual ate it before commencing incubation.

Four of the six nests found in 2001 were first observed prior to hatching. In all four of these, clutch size was two eggs.

Nestling care

A nest with less than one day-old young was observed at 06h30–15h00 on 30 March. Adults made on average 1.09 feeding trips to the nest per hour and initiated a brooding bout after each feeding event. Adults brooded nestlings for 83% (411 minutes) of the 8.25-hour observation and were absent from the nest for only 15% of the time. Mean (± SD) brooding-bout duration, of 12 complete bouts, was 30.2 ± 25.36 minutes (range: 0.23–78.0). At 06h44 a brooding adult stood up in the nest and regurgitated food for its nestlings; regurgitation was not observed subsequently in the day.

Three nests with 10–12 day-old young were observed for a combined total of 29.8 hours. The overall mean (± SD) feeding rate at these nests was 2.96 ± 0.19 feeding visits/hour (range: 2.75–3.14). Feeding adults tended to spend less time perched on the rim of the nest if they did not thereafter brood the young (33.36 ± 21.13 seconds) than if they did so (89.5 ± 85.5 seconds). Mean time spent brooding was 23.33 ± 15.31% of total observation time (range: 10.1–40.1). Mean brooding-bout duration, of 23 complete bouts, was 18.32 ± 12.42 minutes (range: 1.1–52.5).

Adults at two nests, each containing 10–12 day-old nestlings, that were each observed for an entire day (11.03–11.13 hours, between 06h40 and 18h40) exhibited very different patterns of feeding and brooding, possibly due to different rainfall patterns on the observation days (Fig. 1). Adults spent much more time on the nest and fed less frequently on a day with constant rainfall than on a day with rain only in the afternoon. These differences were manifest primarily between mid-morning and early afternoon; brooding and feeding patterns at the two

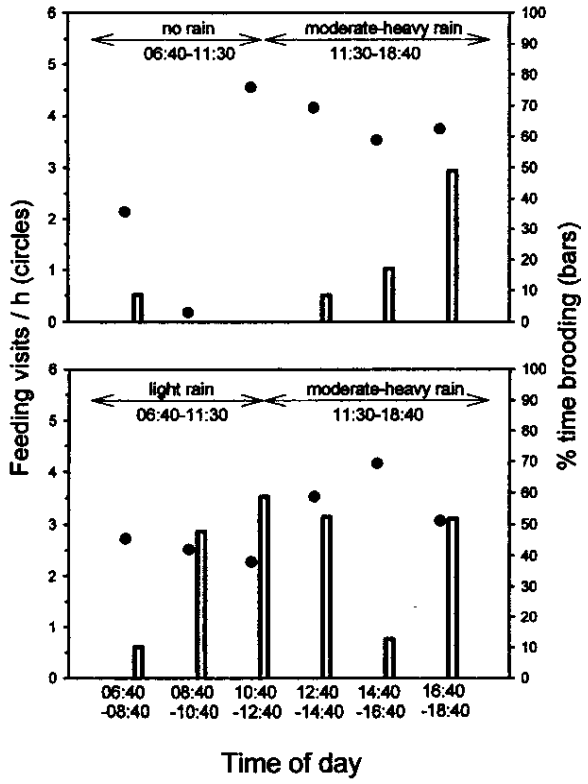

Figure 1. Mean feeding rate and time (as a percentage) spent brooding (during two-hour time periods) by adult *Grallaria guatimalensis* during daylight hours at two nests with 10–12 day-old nestlings. The top panel represents a nest observed on 7 March 2001, a day with no rain between dawn and noon, but constant rain thereafter. The bottom panel represents a different nest observed on 25 February 2001, a day of constant rainfall.

nests were similar during earlier (06h40–08h40) and later (14h40–16h40, 16h40–18h40) periods, irrespective of overall weather patterns (Fig. 1). Typically at this site, at this season, it rains every afternoon and night, but less consistently between dawn and late morning.

During the nestling period adults always arrived at the nests with food (100% of 97 nest visits) and usually fed nestlings while perched on the rim of the nest (Fig. 2). As an adult arrived at a nest, nestlings began begging by stretching their necks skywards and opening their bills, and often appeared to anticipate adult arrival by 0.5–1.5 seconds. Although begging intensity subsided after feeding, nestlings generally continued to beg while the adult remained perched at the nest and until several seconds after the adult departed. Adults often perched at the nest for prolonged periods when

Table 1. Linear measurements and mass change of two *Grallaria guatimalensis* eggs (from the same clutch) over the course of incubation. Regular incubation commenced 12 March; both eggs hatched 29 March.

		Mass		
	Linear dimensions	10 March	15 March	28 March
Egg 1	30.11 x 23.63 mm	8.973 g	8.680 g	7.442 g
Egg 2	29.13 x 23.65 mm	8.612 g	8.340 g	7.279 g

nestlings had difficulties swallowing larger food items. If one or both nestlings could not ingest a food item, the adult would eat it while at the nest. Ten prey items, collected directly from the mouths of two 10–12 day-old nestlings after four feeds by adults, comprised six scarab beetle (Carabidae) larvae and one adult, one large millipede, one 4.5 g earthworm (15 cm long), and one unidentified segmented, cylindrical, red insect larva.

Adult postures while sitting on nests varied over the course of the nesting cycle. Adults incubating eggs and brooding young nestlings sat very low (Figs. 3–4), appeared very deliberate and cautious when arriving at the nest and often remained alert for several minutes after settling onto the nest (Fig. 5). As nestlings grew, adults sat higher in the nest (Fig. 6) and often stood in the nest to shield very large nestlings.

Nestlings

Nestling growth rates and development for *G. guatimalensis* had been described previously from our study site[1]. Previously unnoticed, however, was a moderately strong musk odour of 10–12 day-old nestlings. This odour may occur in nestlings at other ages as well. At present, we do not know the origins of the odour, and we do not know if it serves a function. The odour is not found in the nest (without nestlings), and appears to be associated with the entire nestling (i.e., it is not localised to one part of the bird).

Nest maintenance

During two trips to the nest during egg laying, when adults were starting to incubate periodically but irregularly, an adult took a small amount of nesting material and appeared to add it to the nest lining before settling at the nest. Similar behaviour was also observed during the first five days of regular incubation, in which an adult took a thin, stiff piece of nesting material (possibly a dead leaf petiole) and added it to the nest immediately prior to commencing an incubation bout. As was observed on one occasion during the nestling period, adults occasionally removed small amounts of material from the nest for unknown reasons. Another brooding adult simply moved a piece of material from one part of the nest to another.

During observations at all nests, in the egg-laying, incubation and nestling periods, adults frequently stood up from incubating or brooding positions to probe the lining of the nest with their bills. Both adults were observed to conduct this behaviour, in which birds stuck their heads deep in the nest cup and engaged in rapid probing or pecking movements, such that their bodies appeared to vibrate. Birds often peered into the bottom of the nest before engaging in, and between bouts of, this behaviour (Fig. 7). Although adults occasionally moved eggs or tended nestlings with their bills, they frequently probed the nest lining and would stand from incubation or brooding positions up to ten times per bout in order to do so. We surmise that birds were seeking to locate and remove parasites, possibly eggs or pupae of parasitic flies. To date, however, we have observed no ectoparasites on *G. guatimalensis* nestlings at this site.

In 47 of 50 cases (94%) where an adult was observed to definitely remove a faecal sac from a nest (10–12 day-old nestlings), the adult consumed the faecal sac while perched at the nest. This tendency to eat faecal sacs at the nest, as opposed to carrying them away from the nest, was not an artefact of birds remaining at the nest to commence brooding; only 14 of the 47 visits (30%) during which faecal sacs were consumed culminated in brooding.

Other behaviour

Adults incubating and brooding nestlings occasionally sang softly from the nest. Two song-types were recognised: a soft version of the typical song, which is a trill-like series of hollow notes, and a soft, two-part song that commenced like a typical song, but ended in a series of 7–10 well-defined and louder descending notes with a nasal quality.

Brooding adults occasionally preened their breast feathers while sitting on the nest. While incubating or brooding in the rain, adults shed water from their heads by stretching their necks and shaking their heads rapidly from side to side. Adults often sat on the nest with eyes closed and appeared to sleep while incubating and brooding (Fig. 8), and occasionally and briefly opened their bills widely. Incubating and brooding adults opportunistically reached from the nest and gleaned passing prey, including a myriopod and several small unidentified insects, from surrounding vegetation or the edge of the nest.

Though we have flushed, and have seen natural predators flush[1], numerous adult *G. guatimalensis* from nests, only one performed a fluttering wing display as it departed. This bird, initially perched on its c.0.5 m-high nest, flushed as a person approached to within 2 m. Quivering its wings, which produced a noticeable fluttering noise, the bird flew in a somewhat zigzagging prolonged flight to the ground, where it landed c.3 m away. In response to human movement in the vicinity of a nest (e.g., 25 m away), an attending adult typically froze and stared in the direction of the disturbance (Fig. 9).

Nesting success

Though nests could not be monitored consistently, two of the six were certainly successful, each fledging one young. Of the four unsuccessful nests, two were predated—one with two 9–10 day-old nestlings and one with eggs. At the latter, each of

the two eggs had a small (2–3 mm) square hole cut into the bottom of it, presumably by an insect. (The frequency of egg-boring by insects is unknown, but it has been observed at nests of other species, e.g. Black Phoebe *Sayornis nigricans*, RCD pers. obs.) The yolk and albumin had leaked from these eggs, causing them to glue to the nest lining. Although the adults eventually removed one of these eggs, they continued incubating the other for some time. One nest with two eggs was apparently blown out of its substrate during a wind storm. Unlike most nests, which are low and well supported by 1–2 large and/or several smaller upright stems, this nest was relatively high (2 m) and located away from the main vertical stem, centred on a 3–4 cm diameter horizontal branch, but also supported by 5–10 very small secondary stems. The other unsuccessful nest failed for unknown reasons.

Discussion

Egg-laying behaviour, previously undescribed in the subfamily Grallariinae, was observed for one female *G. guatimalensis*, which laid one egg between 17h05 and 17h15 and then 44–48 hours later the second. Timing was quite late in the day compared to many passerines, which often lay in the early morning (pers. obs.). While early-morning laying avoids the constraints of carrying fully formed eggs during the day, *G. guatimalensis* is primarily terrestrial and flies only irregularly, limiting the constraints of flight on the timing of egg laying. Limited incubation of (or more correctly, sitting on) the first egg between laying events did not result in asynchronous hatching after the 17-day period of regular incubation, suggesting that birds did not begin to heat the eggs until the clutch was complete. The incubation period, previously unknown for *G. guatimalensis*, is identical to that documented for Variegated Antpitta *G. varia* in French Guiana[2]. Although its significance is unclear, the fairly high water loss in eggs (15.5–17.0% of original egg mass) we observed over the incubation period is noteworthy given the extremely wet environment of the study site.

Patterns of nest attendance during incubation and nestling periods were similar to our previous descriptions of *G. guatimalensis* at this site[1]. As expected, brooding by adults decreased and feeding frequency increased as nestlings aged. Variation in daily brooding and feeding behaviour appeared to be influenced by variation in rainfall, but not early or late in the day. Singing from the nest, noted previously in incubating adult Streak-chested Antpitta *Hylopezus perspicillatus*[4], was observed three times, by at least one brooding adult during a day-long nest observation, and also occurred during incubation. One of the two song-types given is unique and very different from typical song, which was also uttered softly from the nest. The significance of the musky odour of nestlings is unknown. Although we are unaware if adults possess a similar, or otherwise distinctive, smell, the characteristic may be unique among nestlings. Of interest, in this respect, was the feeding of a large black-and-yellow millipede to the young. The millipede is fairly common at the site, but has a strong odour of cyanide and was assumed by us to be unpalatable. After heavily mashing the millipede, the adult *G. guatimalensis* fed only half of it to the young. We hope to further investigate if the millipedes provide the source of the musk odour in the young and if other species at the site also feed their young large millipedes.

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Figure 2. Adult *Grallaria guatimalensis* perched on the edge of a nest, waiting to feed two nestlings less than one day old. All paintings by P.R. Martin, from video footage.

Figure 3. Adult brooding two young nestlings. Posture of the adult is typical of brooding, when nestlings are young, and of incubation, when birds sit extremely low in the nest. After arriving at the nest, adults shuffle side to side, each time lowering themselves until this position is attained.

Figure 4. Adult incubating two eggs, showing extremely low position of incubating adults. Note head positioned as low or lower than the rest of its body.

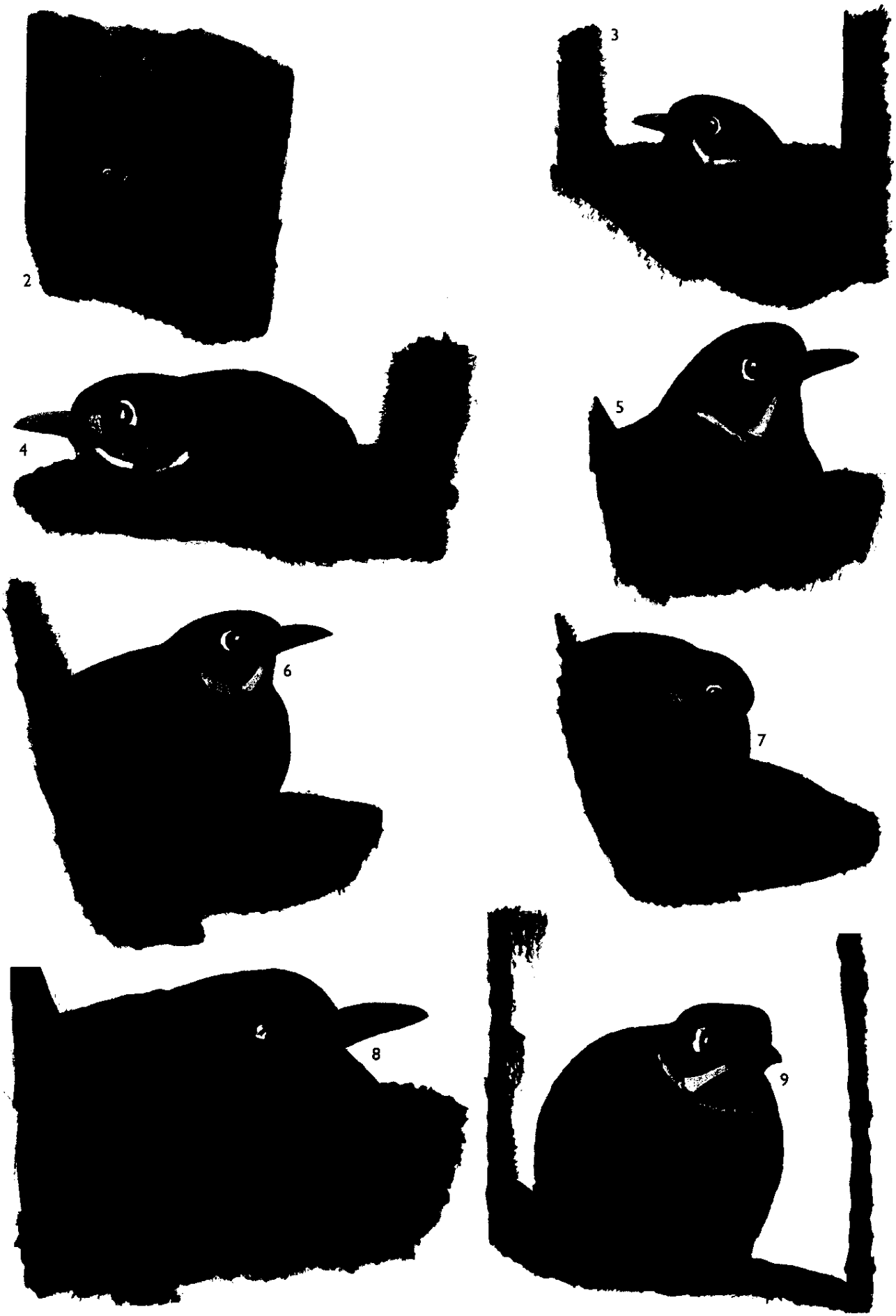
Figure 5. Typical posture of brooding adult immediately following arrival at the nest. Posture is still somewhat erect with head feathers flat on head and neck, alert prior to settling to brood.

Figure 6. Adult brooding 10–12 day-old nestlings, sitting very high in the nest compared to posture typical of incubation and brooding of young nestlings.

Figure 7. Adult with two young nestlings, staring into nest prior to rapid, sewing machine-like probing of nest lining.

Figure 8. Adult brooding young nestlings. Adults often closed eyes for brief periods (1–2 seconds), apparently dozing as they brooded.

Figure 9. Adult with nestlings, holding frozen, alert posture in response to potential danger.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Robert C. Dobbs
Yanayacu Biological Station, c/o 721 Foch y Juan Leon Mera, Quito, Ecuador. Correspondence to: 817 Brentwood Boulevard, Lafayette, Louisiana 70503, USA. E-mail: elaenia@hotmail.com.

Paul R. Martin
Yanayacu Biological Station, c/o Foch 721 y Juan Leon Mera, Quito, Ecuador.

Chelina Batista
Smithsonian Tropical Research Institute, Roosevelt Avenue, Ancon, Balboa, Tupper Building, P.O. Box 2072, Panama.

Hannah Montag
35 High Street, Easton, Bristol BS5 6DW, UK.

Harold Greeney
Yanayacu Biological Station, c/o Foch 721 y Juan Leon Mera, Quito, Ecuador.