

NATURAL HISTORY AND BREEDING BIOLOGY OF THE
RUSTY-BREASTED ANTPITTA
(*GRALLARICULA FERRUGINEIPECTUS*)

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ABSTRACT.—We provide substantial new information on the breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus ferrugineipectus*) from 40 nests during four consecutive breeding seasons at Yacambú National Park in Venezuela. Vocalizations are quite variable in *G. ferrugineipectus*. Nesting activity peaked in April when laying began for half of all nests monitored. The date of nest initiation pattern suggests this species is single-brooded. Both parents incubate and the percent of time they incubate is high (87–99%) throughout the incubation period. The incubation period averaged (\pm SE) 17.0 ± 0.12 days, while the nestling period averaged 13.37 ± 0.37 days. *G. f. ferrugineipectus* has the shortest developmental time described for its genus. Time spent brooding nestlings decreased as nestlings grew, but was still greater at pin feather break day than observed in north temperate species. The growth rate constant based on mass ($k = 0.41$) and tarsus length ($k = 0.24$) was lower than the k for north temperate species of similar adult mass. All nesting mortality was caused by predation and overall daily survival rate (\pm SE) was relatively low (0.94 ± 0.01) yielding an estimated 15% nest success. Received 13 January 2007. Accepted 25 July 2007.

Breeding biology and life history traits of most neotropical birds are poorly known and antpittas are no exception (Krabbe and Schulenberg 2003, Rice 2005). The small antpitta genus *Grallaricula* comprises eight species (Krabbe and Schulenberg 2003). Nest descriptions and scanty breeding information are available for *G. ferrugineipectus*, *G. nana*, *G. flavirostris*, and *G. peruviana* (Krabbe and Schulenberg 2003). The most detailed study to date is that by Schwartz (1957) for the Rusty-breasted Antpitta (*G. f. ferrugineipectus*) where the description of nest and breeding biology was based on only three nests in a forest (850–900 m elevation) south of Petare, Edo. Miranda, Venezuela. Information on the exact length of incubation and nestling stages, parental behavior, predation rates, and nestling growth rates remain unknown. Our objective

is to provide data on these previously undocumented life history traits and other natural history information for *G. f. ferrugineipectus* based on detailed field observations. Field work was conducted during four consecutive breeding seasons from 2003 to 2006 at Yacambú National Park, Edo. Lara, a montane cloud forest area in north-central Venezuela (09° 42' N, 69° 42' W; 500–2,200 m elevation). Means are presented with one standard error (SE) unless otherwise noted.

OBSERVATIONS

Distribution and Habitat.—The Rusty-breasted Antpitta has a disjunct distribution ranging from Venezuela and northern Colombia (subspecies *ferrugineipectus* and *rara*) to northern Peru and western Bolivia (subspecies *leymebambae*) (Ridgely and Tudor 1994, Krabbe and Schulenberg 2003). *G. f. ferrugineipectus* in Venezuela has a wide altitudinal distribution, ranging from 250 to 2,200 m (Giner and Bosque 1998) and inhabits tropical and subtropical areas of the Andes of Mérida and western Lara, Falcón, Yaracuy, Distrito Federal, and Miranda (De Schauensee and Phelps 1978). We worked on this species in Yacambú from its upper distributional limit at 1,600 m elevation down to 1,300 m. We found it mostly in secondary growth wet forest with a closed upper story (7–15 m) and an under-

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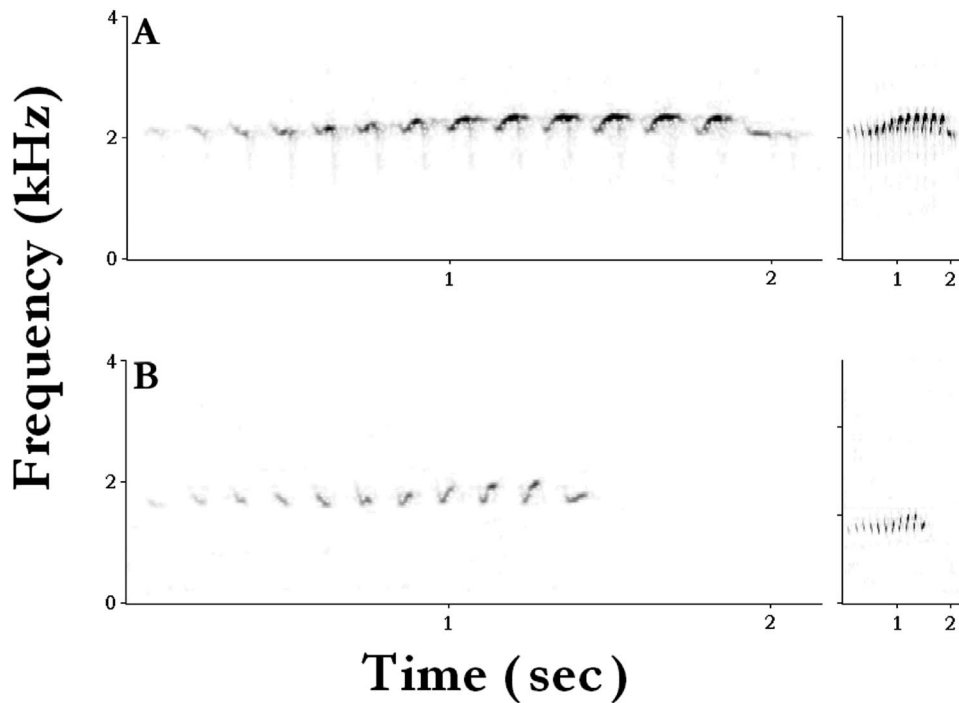


FIG. 1. Vocalization spectrograms of *G. f. ferrugineipectus*. (A) Adult main song (probably male), recorded by J. I. Areta, 13 June 2006. (B) Voice on the nest (unknown gender) from a videotape by L. A. Biancucci, 22 April 2005. Both recordings were during the breeding season at Yacambú National Park, Lara, Venezuela. Spectrograms on the right are reduced in scale to show overall pattern.

growth occupied mostly by vine tangles, small tree saplings, and *Chamaedorea* spp. palms.

Foraging.—Individual Rusty-breasted Antpittas were consistently observed foraging between 0.5 and 2.0 m above ground, but not hopping on the ground like many *Grallaria* spp. (Stiles 1992; A. M. Niklison, pers. obs.). We did not quantify foraging behavior, but most foraging involved hopping along branches, peering at leaves, and sallying to gather flying insects. Schwartz (1957) also reports birds descending from perches to the ground to catch insects and immediately flying back to the perch. Additionally, we had a single observation of a curious foraging behavior where a bird perched on a small branch and vigorously shook it with both feet to flush insects which were then caught by sallying.

Vocalizations.—The Rusty-breasted Antpitta was vocal throughout the day during the breeding season. Singing activity peaked in the early morning and late afternoon. Adults (presumably only males sing, Schwartz 1957)

were recorded singing under natural conditions and after playback with their own voice. The loudsong of *G. f. ferrugineipectus* consisted of a series of 14–17 plaintive and whistled chevron shaped notes (on the sonogram) that increase slowly in pitch, and then descend at a faster rate and ending in one or two distinctive lower pitched and flatter notes (Fig. 1A). The unsolicited loudsong lasted 2 sec and ranged from 1.2 to 2.6 kHz with a high frequency harmonic documented at 14 kHz in some individuals. The large variation in timing and rate of pitch increase prompted Schwartz (1957) to distinguish two loudsongs, and our recordings ($n = 8$) concurred. The loudsongs seem to grade into each other through many intermediates spanning the two extremes (Schwartz 1957 provides a phonetic notation of the voices), and they might be better understood as extremes within a single extremely variable loudsong. Spontaneous vocalizations usually consisted of 14 notes and remained constant after playback or when ex-

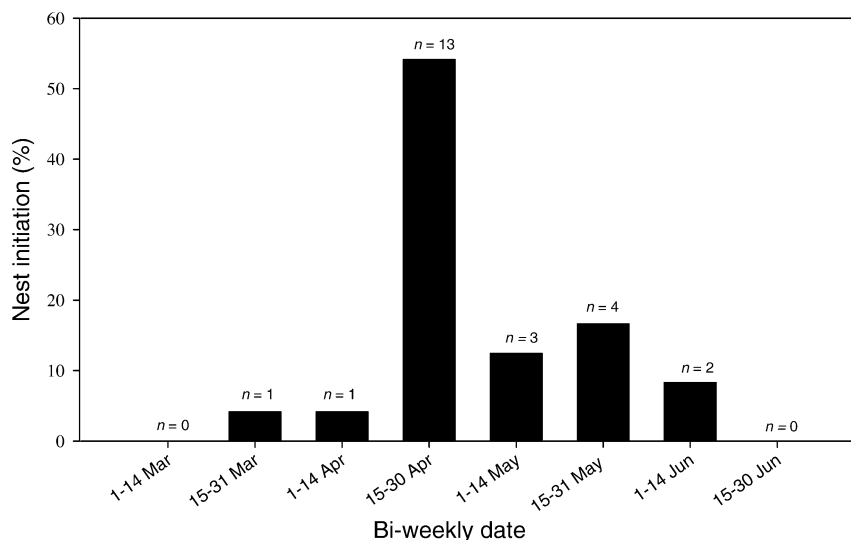


FIG. 2. Percent of nests that were initiated (first egg laid) by date for *G. f. ferrugineipectus* at Yacambú National Park, Lara, Venezuela, March to July, 2003–2006. Only nests for which initiation date was observed are included ($n = 24$).

cited, unlike *G. lineifrons* in which the number of notes decreased from 21 in unsolicited vocalization to 13–15 notes after playback (Robbins et al. 1994). The loudsong of the nominal subspecies at Yacambú differs strikingly from that of the allopatric *G. f. leymebambae* whose loudsong is a monotonous series of whistles (Mayer 2000, Krabbe and Schulenberg 2003). The loudsong of *G. f. ferrugineipectus* recalls that of *G. nana* and *G. lineifrons* in basic pattern, note shape, and frequency range differing most notably in pitch, speed, and length (Robbins et al. 1994; J. I. Areta, pers. obs.).

We recorded a previously unreported shorter, softer, and relatively unstructured and variable song emitted by a bird on the nest during the 2 min that preceded leaving the nest for an off-bout (Fig. 1B). This bird was not immediately replaced by any other and we suspect this might be a contact call eliciting parental switch. A similar soft voice was uttered in a parental switch during incubation in more than one occasion (video recording data). Schwartz (1957) also describes a short single-note call, but we did not hear or record this call at our study site.

Nesting Chronology.—The nesting period for this species was thought to start in mid May and limited to the earliest part of the

rainy season (Schwartz 1957). However, in Yacambú the rainy season spans from mid-April until mid-July. We worked at this site from the beginning of March until early July each year and found that nest building and egg laying started several weeks before the rainy season and continued through June. The peak in nesting activity occurred at the beginning of the rainy season in the last 2 weeks of April when 54% of nests were initiated (Fig. 2). We found 40 nests between March and July for all years combined. The earliest active nest was found empty on 27 March 2006 and had two eggs by 31 March 2006. The latest date of nest initiation was 7 June 2006.

On two occasions, nest building activity was observed within 3 days of predation events and within 10 m of the depredated nests. Given the proximity and timing, we assume these reflect re-nesting attempts, but the pattern of initiation observed (Fig. 2) suggests this species is single-brooded; pairs that successfully fledged young were not observed initiating a new nest in the same season.

Clutch Size and Eggs.—All nests that were occupied ($n = 37$) had two eggs or nestlings similar to that reported by Schwartz (1957). Clutch size in *Grallaricula* varies between one in *G. nana* and *G. peruviana*, and two in *G. ferrugineipectus*, and between one and two



FIG. 3. Top view of the nest and egg of *G. f. ferrugineipectus*, Yacambú National Park. Photograph by A. M. Niklison, 19 April 2005.

in *G. flavirostris* (Holley et al. 2001; Greeney et al. 2004a, 2004b; Greeney and Sornoza 2005).

Eggs were short, sub-elliptical to oval in shape, and usually pale greenish or grayish with variously shaped markings in brown shades over the entire surface. The greenish background color of *G. f. ferrugineipectus* eggs (Fig. 3) is different from the pale coffee-brown with darker brown blotches described for *G. nana* (Greeney and Sornoza 2005), *G. cucullata* (Schonwetter 1967), *G. flavirostris* (Holley et al. 2001), and *G. peruviana* (Greeney et al. 2004a, 2004b). Two clutches had eggs with brownish background color. The pattern of markings closely resembles that of *G. nana* (Fig. 3; and Fig. 1 in Greeney and Sornoza 2005).

We weighed 15 eggs at eight nests between day zero and day 2 of the incubation period using an ACCULAB portable electronic scale (precision 0.001 g). Individual eggs varied from 2.40 to 3.02 g among the eight nests and averaged 2.78 ± 0.05 g, which was $\sim 17\%$ of average adult weight (16.48 ± 0.43 g, $n = 10$). Egg dimensions averaged 1.88 ± 0.13 cm

in length and 1.73 ± 0.15 cm in width (Mitutoyo digital caliper, precision 0.01 mm, $n = 3$). Volume was estimated using Hoyt's (1979) formula ($0.51 \times \text{length} \times [\text{width}^2]$) and averaged 2.84 ± 0.29 cm³.

Nests and Nest Placement.—Nests were unstable and difficult to remove without destroying them, as is common for *G. f. ferrugineipectus* and other *Grallaricula* (Greeney et al. 2004b, Greeney and Sornoza 2005). Nests were in secondary growth areas in microhabitats with abundant vine tangles. Construction was simple consisting of a slightly concave twig platform on top of which black rootlets were knitted in a shallow cup finished with thin and brown rootlets without moss. They were usually supported by slender vines or placed on top of a palm leaf from 0.5 to 2.0 m in height, averaging 1.30 ± 0.14 m high ($n = 17$). Unlike *G. peruviana* (Greeney et al. 2004b), only one adult participated in nest construction.

We measured size of nests for outer diameter (from edge to edge), inner diameter (cup), outer height (exterior bottom-to-top), and inner height (bottom-to-top of cup) of 20 nests

(Fig. 3). Inner diameter averaged 6.0 ± 0.16 cm, outer diameter 10.5 ± 0.30 cm, inner height 2.2 ± 0.15 cm, and outer height 4.36 ± 0.31 cm. Nest shape, size, building materials, and poor support are much like those of *G. nana* (Fig. 1 in Greeney and Sornoza 2005), but differ from *G. flavirostris* and *G. peruviana* which attach their mossy nests to branches (Holley et al. 2001; Greeney et al. 2004a, 2004b).

Incubation Period and Behavior.—We measured duration of incubation periods, when possible, as the number of days between the last egg laid and the last egg hatched (Briskie and Sealy 1990, Martin 2002). Eggs hatched synchronously in all cases, suggesting that incubation began when the last egg was laid contradicting Schwartz's (1957) suggestion that incubation began with the first egg. The incubation period varied from 16 to 17.5 days and averaged 17.0 ± 0.12 days ($n = 4$) (also see Schwartz 1957). *G. f. ferrugineipectus* has the shortest incubation period described for the genus; *G. flavirostris* has an incubation period of 17–21 days (Holley et al. 2001) and *G. peruviana* has an incubation period of 20 days (Greeney et al. 2004b).

We measured parental nest attentiveness (percent time on the nest incubating) and duration of incubation bouts by videotaping nests for 6 to 8 hrs starting within 30 min of sunrise (Martin and Ghalambor 1999, Martin 2002). Both adults share incubation and they exchange bouts on the nest. Nest attentiveness increased mildly ($r = 0.47$, $P = 0.06$, $df = 16$) from day 2 to day 17 of incubation, averaging $94.6 \pm 1.4\%$ overall. However, the increase was due to two nests on day 2 in which both parents stayed off the nest for a long period in the afternoon and caused lower nest attentiveness estimates ($82.3 \pm 0.75\%$). Variability in attentiveness in the first few days of incubation is common in tropical birds (T. E. Martin, unpubl. data). If these two nests are excluded, nest attentiveness did not change from day 2 to day 17 of the incubation period ($r = 0.20$, $P = 0.47$, $df = 14$) and averaged $96.3 \pm 0.95\%$. On and off-bout durations were unrelated to incubation age (both $r < 0.3$, $P > 0.05$). On bouts averaged 66.53 ± 4.44 min, $n = 17$. Nests were nearly continuously occupied.

A general comparison of nest attentiveness

and on-bout/off-bout duration among species of *Grallaricula* is not possible due to the lack of published data. However, information for *G. nana* indicates lower incubation attentiveness (65%, Greeney and Sornoza 2005), shorter on-bouts averaging (\pm SD) 53.8 ± 44.3 min, and longer off-bouts averaging (\pm SD) 10.6 ± 15.7 min than for *G. f. ferrugineipectus*. The incubation day of these measurements was not reported and we cannot provide a more precise comparison.

Adults during incubation performed nest maintenance by arranging edge sticks or inner cup rootlets and by bringing material to the nest when switching, as also observed by Schwartz (1957). Adults frequently rotated their bodies and stood to examine and possibly rotate the eggs, as also observed in *G. nana* (Greeney and Sornoza 2005).

Nestling Period and Brooding Behavior.—We measured the nestling period as the number of days from hatching to fledging. The nestling period varied from 12 to 14 days and averaged 13.37 ± 0.37 days ($n = 4$) similar to the 13-day period reported by Schwartz (1957) but relatively shorter than the reported 14–16 days for *G. flavirostris* (Holley et al. 2001).

Nestlings are naked at hatching and the gape is deep orange. The juvenile plumage is a thick wooly down that is hair-like rather than feather-like. The plumage tract of the head during development is reduced to a single narrow track that resembles a scalp-lock.

Adults provisioned young an average of 3.77 trips/hr ($n = 1$) on the first day of the nestling period, 3.91 ± 1.06 ($n = 3$) on day 2, 4.48 ± 0.07 ($n = 2$) on day 6, and on day 8 (day the pin feather of primary 8 breaks its sheath) they fed 9.08 times/hr ($n = 1$). Both parents brought spiders, butterflies, crickets, cockroaches, larvae, and beetles as feeding items (this study; Schwartz 1957).

The percent of time spent brooding during the nestling period was averaged across bouts for each nest and then averaged across nests, with the SE reflecting this cross-nest mean. Brooding time averaged 98% ($n = 24$ bouts, 1 nest) on day 1, $84 \pm 3\%$ ($n = 68$, 3 nests) on day 2, $90 \pm 3\%$ ($n = 52$, 2 nests) on day 6, and 61% ($n = 9$, 1 nest) on day 8, pin-break day. Time spent brooding is higher ($P < 0.001$) than published for some north-tem-

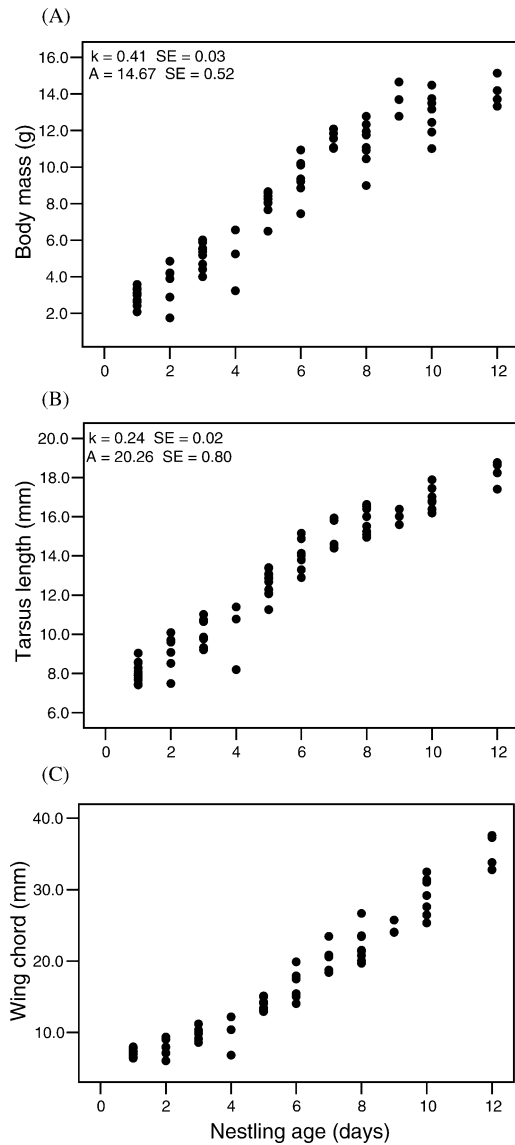


FIG. 4. Nestling measurements of *G. f. ferrugineipectus* at Yacambú National Park plotted against age: (A) Mass, (B) Tarsus length, and (C) Wing-chord. Growth rate constant (k) and asymptote (A) are indicated for mass and tarsus.

perate birds; for example the Song Thrush (*Turdus philomelos*) broods only 29% of the time on the day that pin feathers break their sheaths (Hill et al. 1999).

Nestling Growth.—We measured nestling tarsus length and wing chord (Mitutoyo digital calipers, 0.01 mm precision) and weighed nestlings (ACCULAB digital electronic

scales, 0.001 g precision). We estimated growth rate using the formula $W(t) = A/\{1 + e^{[-K(t-t_i)]}\}$, where $W(t)$ refers to mass or tarsus length at day t , k is the growth rate constant, A is the estimated asymptotic mass or tarsus length, and t_i is the inflection point of change from accelerating to decelerating growth, following Ricklefs (1967). The growth rate constant for mass (Fig. 4) was lower than the k for unrelated north temperate passerine species that averaged $k = 0.52 \pm 0.05$ ($n = 4$) for a similar adult weight (16.2–17.5 g) based on data in Remeš and Martin (2002). Nestlings (10–13 days of age) did not “play dead” during measurements in contrast to Schwartz (1957). Nestling weight on day 12, the day before normal fledging averaged 14.09 ± 0.39 g ($n = 4$) which was 85% of adult body mass. The Rusty-breasted Antpitta fledged with a larger relative body mass ($t_3 = 3.81$, $P = 0.032$) than similar-sized but unrelated north temperate species $75 \pm 5\%$, $n = 4$ (Remeš and Martin 2002). This may reflect the longer ($t_3 = 10.33$, $P = 0.002$) time spent in the nest compared with north temperate species.

Nest Predation and Success.—We did not find all nests during nest-building; 16 nests were found during nest-building, 19 during incubation, and 5 during the nestling stage. Consequently, we calculated daily survival rates using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981). Three nests were abandoned during building and one was lost due to investigator disturbance; these were excluded from the Mayfield estimates. Twenty-five of the remaining 36 nests were lost to predation and the rest were successful. One nest was depredated during the laying period, 18 during incubation, and 6 during the nestling period. Overall daily survival rate was 0.94 ± 0.012 ($n = 409.5$ exposure days, 36 nests). Daily survival rates were 0.931 ± 0.067 for the laying period, 0.929 ± 0.016 for the incubation period, and 0.958 ± 0.017 for the nestling period. Only 15% of *G. f. ferrugineipectus* nests were successful as estimated by the Mayfield method. North temperate passerine species have a higher estimated nesting success ($t_{17} = 6.876$, $P < 0.001$), averaging $42.43 \pm 0.040\%$ ($n = 18$) (Martin 1992).

DISCUSSION

Our data are typical for many tropical species, where they exhibit a slower pace of life

compared with north temperate species, including small clutch size, slow development during both incubation and nestling stages despite high parental care, and lower nesting success (Martin 1996, Martin et al. 2000, Martin 2002, Martin et al. 2007). Contrary to views that these traits might reflect long breeding seasons (reviewed by Martin 1996), the breeding season was similar in length to north temperate systems, and the species did not appear to be multi-brooded suggesting that alternative explanations need to be sought. The behavior of sharing incubation duties by both males and females is relatively uncommon in north temperate passerines but common in a number of endemic tropical groups (Martin et al. 2007). The high brooding attentiveness late into the nestling stage may also be common in tropical endemics, but these behaviors have been neglected and deserve further attention.

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