ABSTRACT.—The Spotted Barbtail (Furnariidae) is poorly studied but shows some extreme traits for a tropical passerine. We located and monitored 155 nests to study this species for 7 years in an Andean cloud forest in Venezuela. Spotted Barbtails have an unusually long incubation period of 27.2 ± 0.16 days, as a result of very long (3–6 hr) off-bouts even though both adults incubate. The long off-bouts yield low incubation temperatures for embryos and are associated with proportionally large eggs (21% of adult mass). They also have a long nestling period of 21.67 ± 0.33 days, and a typical tropical brood size of two. The slow growth rate of the typical broods of two is even slower in broods artificially reduced to one young. Nonetheless, the young stay in the nest long enough to achieve wing lengths that approach adult size. Received 24 January 2014. Accepted 25 April 2014.

Key words: breeding biology, furnariid, growth rate, incubation attentiveness, Venezuela.

Intra- and inter-specific variation in life-history traits have a major role in population and community ecology (Roff 2002, Sæther et al. 2004). However, the cause for life history variation remains one of the biggest unsolved questions for theoretical and field ecologists (Roff 2002). Solving the question is hampered in part by the lack of information for a great number of species, especially in the tropics. Detailed studies of life histories of poorly-studied tropical species can aid development of hypotheses to explain variation, especially if species show extreme variation in life history traits (Martin 1996, 2004). When compared to other Neotropical passerines, the Spotted Barbtail (Premnoplex brunnescens) shows unusually long duration of its incubation period as well as unusual incubation behavior (Martin et al. 2007, Martin and Schwabl 2008, Greeney 2009). The aim of this study is to contribute detailed information on broader aspects of the breeding biology of this member of a large family of passerine birds, the Furnariidae.

Furnariidae (Ovenbirds) is one of the most diverse Neotropical families, with about 288 species (Remsen et al. 2014), and nest types have shown interesting diversification (Zyskowski and Prum 1999). Representatives of this family are found in a variety of habitats, from coasts to arid savannas and humid forests, covering a geographic range, from Mexico to Argentina (Vaurie 1980). Spotted Barbtails are found at elevations from 700–3,000 m and distributed from Costa Rica to Bolivia (Skutch 1967, Hilty 2003, Restall et al. 2007). In Venezuela, their distribution extends across three major mountain systems and contains two subspecies. Premnoplex b. brunnescens is found in most of the Andes and the Serranía de Perijá, while P. b. rostratus is found in the northern Andes and coastal Cordillera (Hilty 2003, Restall et al. 2007). The information reported here was collected in a transition region between the Andes and the north-central portion of Venezuela, and most likely comprises the range of subspecies rostratus (Hilty 2003, Areta 2007, Restall et al. 2007).

STUDY SITE AND METHODS

The study was conducted in Yacambú National Park (9° 24’ N, 69° 30’ W) in Lara State, western Venezuela as part of a broader study of life history variation in mid-elevation tropical birds (Martin et al. 2006, 2007, 2011). The fieldwork was restricted to cloud forest habitat between 1,350–2,000 m. The mean ambient temperature is 20.6 °C, and precipitation varies from 1,700–2,300 mm during the rainy season that lasts from April to November (Parkswatch 2003).

Data were collected during seven field seasons (Mar–Jul), from 2002–2008. Nests were found by means of systematic search and subsequently monitored every other day to determine status, but we checked them daily or twice-daily around stage-changing events, such as laying, hatching or fledging (Martin and Geupel 1993; Martin et al. 2007, 2011).
We marked eggs by laying order and weighed them to the nearest 0.001 g with an ACCULAB (Elk Grove, IL) portable electronic scale. Day zero of incubation was defined as the day the last egg of the clutch was laid (Martin et al. 2006). We also marked nestlings’ legs with non-toxic colored markers or colored plastic strips, and measurements were taken every other day starting the day of hatch (day 0) or one day after (day 1) the eggs hatched (Martin et al. 2011). Measurements included mass (as described for eggs), wing-chord, tarsus and eighth primary feather length using a Mitutoyo (Kingsport, TN) digital caliper. We calculated growth rates by following Remes and Martin (2002), and nest predation and survival rates were calculated following Mayfield (1961, 1975) and Hensler and Nichols (1981). We used a ruler to measure the size of nests based on the dimensions characterized in Figure 1.

We video-recorded incubation behavior of parents during three stages: early, middle, and late incubation. The incubation period was calculated as the difference in days between last egg laid and last egg hatched (Martin et al. 2007) and the corresponding stages defined as one third of the total period length each. Also, we video-recorded parental behavior during three nestling stages defined as: before pin-break, pin-break day, and after pin-break, which correspond to days 0–9, 10–11 and 12–27, respectively, for Spotted Barbtail nestlings (this study). Pin-break day is defined as the day primary feathers start to emerge from their sheaths; timing is usually easy to predict one day in advance as the tips of sheaths

![Diagram of a Spotted Barbtail’s nest](image)

FIG. 1. Diagram of a Spotted Barbtail’s nest, and means ± SE (numbers of nests measured) of measurements taken.

- Inside cup height: 30 ± 0.14 mm (25)
- Inside chamber height: 97 ± 0.03 mm (12)
- Outside cup height: 68 ± 0.22 mm (29)
- Inside cup diameter: 59 ± 0.14 mm (26)
- Outside cup diameter: 99 ± 0.25 mm (10)
- Outside total height: 171 ± 0.45 mm (12)
Video-recordings of nests were made for 6–9 hrs, starting from daybreak, and from a distance of at least 5 m from the nest. We transcribed data collected by these means where time of each behavioral observation or event was recorded and used for estimating frequency and duration of behaviors (Martin et al. 2007, 2011).

Egg temperatures were measured by inserting a thermistor on the first or second day of incubation into the center of an egg through a small hole sealed with glue (Weathers and Sullivan 1989, Martin et al. 2007), which made the egg inviable. The wire was threaded through the nest and connected to a HOBO Stowaway XTI datalogger (Onset; Bourne, MA) that recorded temperatures every 12–24 secs for 5–7 days per nest. Nests with probed eggs remained undisturbed from regular monitoring and filming (i.e., not visited by researchers except to change data loggers), because fate of the nests were recorded through the loggers if they failed.

We captured adults by systematic mist-netting, as well as some target netting at the nest by using playback recordings. We measured adult mass and took notes about morphological features and breeding status.

RESULTS

Nest and Territory.—Spotted Barbtails’ nests consist mostly of moss and dark rootlets, giving a dark brown or greenish brown appearance. The nests are generally attached to rocks, roots, or logs over flowing water, where they remain well-camouflaged (Fig. 2). Nests are domed in shape with a concealed tubular entrance at the front bottom and have a small brood chamber with a frontal elevated cup edge (Fig. 1). Among nests, sizes of diverse measurements were quite similar, as reflected by small standard errors (Fig. 1).

Active nests were commonly found close (within 20 m) to old, unused, or unfinished nests. Up to four nests per territory were observed. Less finished nests (and old ones) are sometimes used
as roosting nests, especially during pre-breeding season. Pair members were captured simultaneously when playback was used during target netting, indicating territorial response of males and females. A few nests were restored and used for more than one season. However, nests were rarely re-used within a season, and only when the nest was abandoned during the laying stage and not depredated.

Reproductive Season.—Initiation of breeding was foreshadowed by small changes in previously inactive old nests or incomplete fresh ones (rarely was construction witnessed from the inception). For example, birds began lining the cup (first clue observed), building up the front side of the cup that faces the entrance, and elongating the dome that covers the entrance well before laying the first egg. These improvements were made slowly, with nest building or nest reconditioning extending for 4–6 weeks prior to egg-laying.

Initiation of breeding (the day the first egg is laid) began in late March and ended by middle June, with most breeding activity from late April to early June (Fig. 3). Mean nest initiation was May 11 ± 1.88 days (n = 130).

In every Spotted Barbtail’s nest that we found, the barbtails laid two white eggs before beginning incubation (n = 111). The eggs averaged 3.533 ± 0.018 g (n = 115) on days 0–2 to represent 21% of adult body mass (16.7 ± 0.13, n = 38). Barbtails would occasionally re-nest following early failure of a first attempt, usually in early to mid-June.

Incubation Period.—Incubation lasted 27.2 ± 0.16 days (n = 16) for nests where we observed the exact day the last egg was laid and the exact day that eggs hatched. This long incubation period was associated with low nest attentiveness during the day (percent time on the nest). Even though incubation is bi-parental in this species, the eggs are left un-attended for 3–6 hrs every day. This long off-bout generally starts in late morning (Martin and Schwabl 2008), and this behavior persists even during late incubation. However, nest attentiveness increased across the incubation period (Fig. 4A; ANOVA, $F_{2,57} = 6.6$, $P = 0.003$). The long period of absence from the nest by both parents each day caused egg temperature to fall to ambient temperature, where the embryos experienced temperatures between 18–20 °C.

![FIG. 3. Seasonal distribution of nest initiation (date the first egg is laid in a nest) for the Spotted Barbtail at weekly (7-day) intervals (n = 130 nests).](image-url)
FIG. 4. (A) Average nest attentiveness (% time spent incubating) of Spotted Barbtails across three periods of incubation: early (days 1–6), middle (days 10–17), and late (days 21–28). Sample sizes reflect numbers of nests and different letters reflect different means (LSD, $P < 0.05$). (B) Average ($\pm$ SE) 24-hr egg temperature relative to day of incubation (day 0 = day the last egg was laid).
during most (generally $> 70\%$) of the long off-put (see fig. 3 in Martin and Schwabl 2008). As a result, average 24-hr egg temperature was quite cold during early incubation (Fig. 4B); temperatures during later incubation were not obtained because of nest predation.

**Nestling Period.**—Both eggs hatched in all nests, except for nests in which eggs were probed for temperature. The rate of feeding visits increased with nestling age, and was greater for broods of two nestlings than single nestlings (Fig. 5A; ANOVA, Nestling age: $F_{1,44} = 66.1, P < 0.001$; Brood size: $F_{1,44} = 20.2, P < 0.001$). The percent of time that parents spent brooding nestlings decreased with nestling age, but was not related to brood size (Fig. 5B; ANOVA, Nestling age: $F_{1,44} = 92.9, P < 0.001$; Brood size: $F_{1,44} = 0.5, P = 0.5$). Brooding ended at day 10–11 which coincides with pin-break day. Nestlings fledged from the nest 22 days after hatching in both nests in which we obtained exact day of hatch and fledging. Fledglings resembled adults in mass and plumage pattern.

Nestlings exceeded adults in mass at pin-break (days 10–11) (Fig. 6A). Nestling mass peaked at day 17, 4–5 days prior to fledging, when they averaged 20.319 ± 0.430 g ($n = 13$) and weighed 121% of average adult mass. Recession of nestling mass after day 17 caused them to approach adult mass at fledging (Fig. 6A). The growth rate constant for mass based on the entire nestling period is $k = 0.329 ± 0.008$ (Fig. 6A) with asymptote ($A$) = 20.866 ± 0.185. If we restrict estimation for the period until they reach adult mass (day 9), the resulting growth rate estimate $k = 0.331 ± 0.016$ remains quite similar. The growth rate constant for broods that had been reduced to one young from temperature-probing had slower growth ($k = 0.286 ± 0.016$) than normal broods of two young ($k = 0.336 ± 0.008$).

The growth rate constant based on tarsus length was slower, and tarsi achieved adult size by about day 14 (Fig. 6B). The growth rate constant based on wing-chord was slowest and wings were 87% of adult size at day 21, the day before fledging, in the only nestling measured at this age (Fig. 6C). Two other nestlings had wings this long on day 19. Wings grow about 3 mm a day at this age, indicating that wing size at fledging exceeds 90% of adult size. This relative size is proportionally longer than for any passerines studied in a north temperate site and suggests fledglings may have relatively good flight abilities that aid survival (Martin 2014).
March–June, but certainly suggests a punctuated main season.

This species showed the longest incubation period associated with the lowest average 24-hr egg temperature among passerines at our Venezuelan site (Martin et al. 2007). The next longest incubation periods among passerines at this site were two other furnariids, *Philydor rufum* and

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**FIG. 5.** The change with nestling age in (A) rates (visits/hr) that parents visit the nest to feed nestlings and (B) brooding behavior (% time spent brooding). Open symbols reflect broods of a single nestling, while closed symbols reflect broods of two nestlings.
Anabacerthia striaticollis, which had incubation periods of 24.0 days \( (n = 2) \) and 23 days \( (n = 1) \), respectively (TEM, unpubl. data). However, a fourth furnariid, Synallaxis cinnamomea, had an incubation period of 19.2 days \( (n = 4; \) Martin et al. 2014) that was more similar to other passerine species at this site (see Martin et al. 2007, 2013). Moreover, study of other Synallaxis spp. in

**FIG. 6.** Relationships of (A) mass, (B) tarsus length, and (C) wing chord length plotted against age for Spotted Barbtails and their estimated growth rate constants \( (K) \). The dashed lines represent mean adult sizes.
tropical Brazil found even shorter incubation periods (e.g., Rubio and Pinho 2008, Marini et al. 2012). Thus, not all furnariids exhibit incubation periods in the mid- to high-20 days, but the scant data here for Spotted Barbtaills and two other previously unstudied species suggest that long incubation periods may not be uncommon among furnariids.

The low egg temperature in the Barbtail was caused by low nest attentiveness during their unusually long mid-day off-bouts (Martin and Schwabl 2008), as also observed in Ecuador (Greeney 2009). Spotted Barbtaills had the lowest incubation attentiveness of any species at our Venezuelan site (Martin and Schwabl 2008). The long incubation periods for the two other furnariids at our site may reflect that irregular incubation behaviors are common in furnariids (see Skutch 1996). Yet, even longer off-bouts up to 8 hrs have been observed in some tropical passerines in Asia that do not have bi-parental incubation (Martin et al. 2013). The low attentiveness despite bi-parental incubation duties in Spotted Barbtaills is surprising and may be favored by high adult survival to reduce daily energetic costs of incubation, allow more time to maintain individual physiological quality, and reduce predation risk of adults (Martin 2002, Martin et al. 2007, Martin and Schwabl 2008, Arnold et al. 2012). Unfortunately, our capture and recapture rates of this species were too low for a reasonable estimate of survival, because we did not net in the steep creek valleys that they occupied. However, we note that one individual banded in the second year of the project was still alive at the end of the project, 6 years later. Nonetheless, the long incubation period exposes the embryos to increased predation risk and the causes for why parents are willing to allow such increased mortality risk remain to be investigated.

The proportion of egg mass to adult body mass (21%) in this species was one of the highest at our field site (Martin et al. 2006, Martin 2008), second only to Mérida Tapaculo which also nested in steep creek valleys (Decker et al. 2007). The large size of the eggs may slow cooling of eggs a bit, but they reach ambient within a few minutes of adults getting off the nest (see Martin and Schwabl 2008), and the large egg size will also slow rate of warming once a parent gets back on (see Turner 2002). The eggs sit at ambient temperature for most (generally > 70%) of the very long off-bout that parents take each day (Martin and Schwabl 2008). The low temperatures associated with the low attentiveness (Fig. 4) incur energy costs to the embryo (i.e., Olson et al. 2006) and may require large eggs with larger yolk and protein reserves to offset these energy costs (Martin 2008).

Long on- and off-bouts may also reflect an incubation strategy that reduces parental activity at the nest to minimize attracting visually-oriented predators (Weathers and Sullivan 1989, Conway and Martin 2000). Barbtaills experienced a relatively low nest predation rate among the species that we studied at this site (see Martin et al. 2006, 2007). The enclosed nests of Spotted Barbtaills keep the contents well hidden from visual predators compared to open cup nesters and could help reduce predation risk (Auer et al. 2007), but the low parental activity at nests may also facilitate lower nest predation risk.

Nestlings grew relatively slow compared with other species at our field site, and only other suboscines showed as slow or slower growth (Martin et al. 2011). Growth rate was slower for brood sizes of one than for normal broods of two young, suggesting a decrease in adult effort when brood size is reduced. This reduction in growth rate with decreasing brood size was typical of other tropical species, and opposite to temperate species (Martin et al. 2011). The fat-loading whereby young exceeded adult mass for roughly half of the nestling period (i.e., Fig. 6A) is typical of species with safe nests or variable food delivery (Remes and Martin 2002) and was not observed in other passerines at this site with higher nest predation risk (e.g., Cox and Martin 2009). Even a small flycatcher did not show fat-loading (e.g., Goulding and Martin 2010), whereas flycatchers often exhibit fat-loading in the temperate zone (Remes and Martin 2002). Young remained in the nest until wings were nearly adult size, which is longer than for temperate species, and may strongly facilitate survival after fledging (Martin 2014). Flight abilities at fledgling may also facilitate the ability of fledglings to avoid falling in the water below the nest (J. I. Areta, pers. comm.). Whether such long wings are typical of tropical birds in general, or associated with the unique characteristics of this species, remains to be studied.

No major differences in reproductive biology were found between Venezuelan populations and reported estimates from Ecuador (Greeney 2008b, c, 2009, 2010), with the exception that the latter
seems to show more variability in lengths of incubation and nestling periods and also in duration of incubation off-bouts. Nestling growth showed a similar growth constant ($K = 0.368$ for Ecuador), but we found a higher asymptote at our study site ($A = 19.75$ versus $A = 20.866 \pm 0.185$ for Ecuador vs Venezuela, respectively). Bimodal breeding, as observed for the Ecuadorian population (Greeney 2008b, c, 2009, 2010), is a phenomenon not studied at our site because of the duration of our field season. Bimodal breeding might occur but will require further efforts that could also provide additional information about the natural history of this still enigmatic species. Ultimately, the unusually long off-bouts during incubation in a species where both parents incubate and the long embryonic development highlight the interesting nature of this species and encourage further study of causes of this variation, as well as study of more members of the diverse Furnariidae.

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LITERATURE CITED


