ORIGINAL ARTICLE

Unusual incubation rhythms the Spotted Barbtail, *Premnoplex brunnescens*

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Abstract The Spotted Barbtail (*Premnoplex brunnescens*) inhabits the understory of humid montane forests in Central and South America. Apart from basic information on eggs and nest form, little has been published on its breeding ecology. Using temperature sensors in nest cups, I have collected data on the diurnal patterns of egg-coverage from three nests in eastern Ecuador and reveal a remarkable incubation rhythm. After providing near-constant coverage during the morning, adults leave the eggs unattended for most of the afternoon, returning to the nest only in the late afternoon. The mean duration (±standard deviation) of this period of absence, across the entire incubation period at three nests, was 6.4 ± 1.9 h. These results are discussed in relation to their physiological and ecological significance.

Keywords Andes · Behavior · Furnariidae · Life history evolution · Parental care

Introduction

Understanding the evolution of life-history traits in animal species has been the focus of intensive research (Ricklefs and Wikelski 2002; Roff 1992); in this context, factors driving nesting strategies in birds has been subjected to intense study (Martin 1996). Factors such as food availability, ambient temperature, seasonality, fecundity, longevity, predation, and parasite loads are all thought to affect avian nesting strategies (e.g., Chalfoun and Martin 2007; Conway and Martin 2000b; Ghalambor and Martin 2001; Martin 2002; Martin et al. 2001). In order to maximize reproductive success, adult birds are thought to balance trade-offs, such as egg temperature and development time with predation risk and energy expenditure during incubation. Thus, the patterns of egg attendance exhibited by a wide variety of avian species are clearly affected by complex interactions of multiple ecological, physiological, and evolutionary traits. While comparing patterns among many similar species may be very useful in elucidating the underlying mechanisms driving incubation rhythms, it is the extreme the examples which provide us with significant insight (Booth and Jones 2002; Carey 2002; Lill 1979).

The Spotted Barbtail (*Premnoplex brunnescens*; Passeriformes: Furnariidae) is an inconspicuous bird inhabiting the interior of montane forests situated between 600 and 3000 m a.s.l. from Costa Rica southward to central Bolivia (Hilty 2003; Hilty and Brown 1986; Remsen 2003; Ridgely and Greenfield 2001). Adults, alone or with flocks, actively glean and probe for arthropods on branches, bark crevices, epiphytes, dead leaves, and tree trunks, usually within several meters of the ground (Areta 2007; Remsen 2003). While the taxonomic placement of *Premnoplex* barbtails has been debated, recent molecular data suggest they form a monophyletic clade with *Margarornis* (Irestedt et al. 2006).

Spotted Barbtails build globular, mossy, ball-shaped nests with a downward-facing tubular entrance (Areta 2007; Greeney 2008a; Marín and Carrión 1994; Skutch 1967). Nests are built in a wide variety of situations ranging from earthen or wooden cavities to suspended

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clumps of moss, almost exclusively directly over streams and below 5 m (Greeney 2008a). While the nest attachment method varies, the nests show very specific orientations that are directly related to the stream flow below the nest (Greeney 2008b). Two eggs, laid at 48-h intervals, are incubated by both parents for 27–31 days (Greeney 2008c). Other than these basic aspects of nesting biology, little has been published on parental care or incubation behaviors. Here I describe the unusual incubation patterns of Spotted Barbtails in northeastern Ecuador.

Materials and methods

From May 2001 to November 2007, I studied nests of Spotted Barbtail (hereafter barbtail) at the Yanayacu Biological Station and Center for Creative Studies (0°36′S, 77°53′W), which is located adjacent to the Cabañas San Isidro reserve, 5 km west of Cosanga, Napo Province, Ecuador. All nests were situated directly above fast-flowing mountain streams, in primary forest, at elevations ranging from 1900 to 2100 m a.s.l.

During each visit to barbtail nests during the incubation period ($n = 344$), I recorded the time of day, to the nearest 15 min, and noted the presence or absence of an incubating adult. At three nests, I placed HOBO dataloggers (Onset, Pocasset, MA) to monitor the entire incubation period. The probes were positioned 1–2 mm below the inner surface of the nest linings, while the external probe was placed inside a nearby cavity, under leaf litter, or in a similarly sheltered location. The loggers were programmed to record temperatures every 2 min. The difference between internal and external probe measurements was then taken as an indicator of the duration of adult presence and absence from the nest, respectively.

A tripod-mounted camera placed 5–8 m from the nests was used to videotape adult activity during the morning and evening on 6 days at each of four nests, while the nest lining temperatures were simultaneously being recorded at three of these with a data logger. The video data were used to directly record the presence of adults in the nest, providing both corroboration and facilitating interpretation of the logger data. The loggers were inserted into the nests either just before clutch initiation or soon after clutch completion. Of the three nests monitored through the entirety of the incubation, one held eggs from 20 September to 19 October 2006, one from 5 November to 6 December 2006, and one from 22 October to 20 November 2007. As a measure of diurnal percentage incubation, I included the period between 0600 and 1800 hours, roughly sunrise to sunset at my study site, which was a time interval comparable to those reported in other studies on avian incubation in the area (e.g., Greeney 2006; Greeney et al. 2006, 2008).

Results

The data compiled from 344 visits to 60 different nests during the incubation period suggested a striking pattern of diurnal incubation (Fig. 1). This pattern was subsequently explored in more detail using the temperature data retrieved from probes inside nests and from the video images. At two of three nests with inserted data loggers, incubation lasted 27 days from clutch completion. At the third nest, both eggs hatched after 29 days (Table 1). At the two nests with shorter incubation periods, adults did not spend the night on the nest until after the second egg was laid. At the third nest, no adult spent the night on the nest until the day after clutch completion, leaving the nest at 1830 hours on the day the second egg was laid and not returning until around 0615 hours the following day. Adults left the nest in the middle of the night on three occasions, twice at the nest with an extended incubation and once at another nest. In both cases at the former nest, they did not return to the nest until after 0600 hours the following morning, having left the nest at 0330 and 0500 hours, respectively. At the other nest, the adult left at 0115 hours, but returned after 40 min. At the nest where the adult left the nest at 0330 hours, 8 days after clutch completion, the internal nest temperature dropped to 12.9°C (slightly below ambient) before the adult returned in the morning. Both eggs were showing visible signs of development at this point, and both eventually hatched. Video evidence confirmed that both adults participated in incubation during the day, usually switching places at the nest, leaving the eggs uncovered for less than 5 min. Based solely on the datalogger readings, I was unable to detect most adult switches during the morning and afternoon. Adults generally switched places at the nest two to five times in the morning and one to two times in the afternoon.
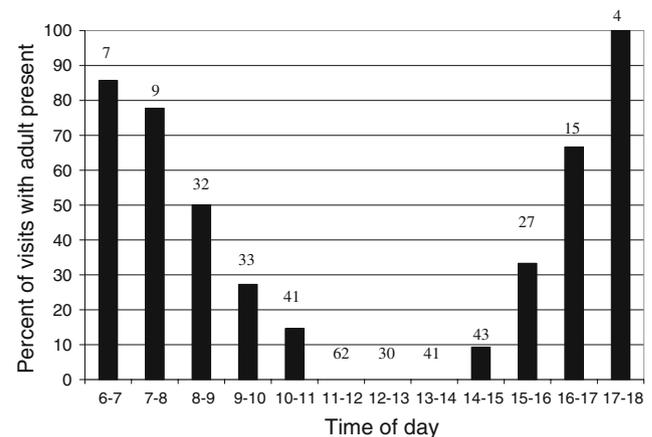

Fig. 1 Percentage of nest checks in which an adult Spotted Barbtail (*Premnoplex brunnescens*) was found incubating in relation to time of day. Sample sizes (number of nest visits) are given *above each bar*

Table 1 Temperature readings of nest, nest and incubation parameters, and adult presence at the nest

Nest no.	Incubation dates	Mean mid-day off-bout duration (h)	Percentage total incubation (0600–1800 hours)	Percentage incubation after day 10 (0600–1800 hours)	Incubation period (days)	Mean temperature increase inside nest (°C)
1	20 September–19 October 2006	6.0	52	62	27	3.2
2	5 November–6 December 2006	6.9	42	51	29	3.3
3	22 October–20 November 2007	6.5	57	54	27	3.0
Grand mean		6.4	47	56	27.7	3.15

Incubation rhythms were characterized by nearly a 100% coverage in the mornings and evenings, with an extended period of absence in the interim period (Figs. 2, 3, 4). Across the entire incubation periods at all three nests, mid-day absences ranged in duration from 4.2 to 9.9 h [mean ± standard deviation (SD) 6.4 ± 1.9 h]. At none of the nests did the mid-day absence consistently last less than 6 h before day 10 of incubation. Mean (±SD) percentage diurnal coverage of the eggs from clutch completion to hatching, across all three nests, was 47 ± 5% (see Figs. 2, 3 and 4). Mean percentage coverage from day 10 through hatching was 56 ± 6% (Table 1). After clutch completion, the daily percentage incubation gradually increased, with little variation between nests, and with the maximum percentage diurnal incubation never surpassing 79% (Fig. 5).

During the incubation periods of all three nests fitted with a temperature probe and viewed with a video camera, the mean ambient temperatures outside the nests was 14.0°C (range 6.6–15.3°C). The internal nest temperatures across the incubation period were on average 3.2°C warmer than the temperature outside the nest, despite the fact that internal temperatures generally dropped to ambient after only 2–3 h of adult absence (Table 1). Because the probes were not in contact with the eggs but were situated in the nest lining, the temperature measurements do not reflect true incubation temperatures. However, the video footage confirmed the correspondence between elevated temperature readings and adult presence at the nest. Probe readings in unoccupied nests (prior to egg laying) showed that internal and external temperatures were identical, with a positive correlation over time, revealing that the nests themselves did not alter ambient temperatures. The duration of the mid-day off-bout was negatively correlated with all five of the following variables: mean diurnal temperature (0600–1800 hours), mean nocturnal temperature the night before (1800–0600 hours), mean morning temperature (0600–1000 hours), mean mid-day temperature (1000–1400 hours), mean afternoon temperatures (1400–1800 hours). In a step-wise regression, however, only mean mid-day temperature explained more than 14% of variation

in off-bout length ($r^2 = 0.1699$). Mean night-time temperatures explained less than 0.5% of observed variation ($r^2 = 0.004$). Thus, cooler diurnal temperatures were weakly associated with longer off-bouts.

Discussion

Skutch (1967) provided researchers with a first glimpse into the unique incubation behavior of the Spotted Barbtail. During two separate observations of a barbtail nest in Costa Rica, Skutch (1967) noted near-constant coverage of the eggs during the morning, followed by periods of neglect lasting over 2 h. On neither occasion was he able to remain at the nest to document the birds' return but, given the observations reported here, it is likely they were absent for most of the day. This behavior suggests that the incubation rhythms observed in the present study may not be unique to this population. The 27- to 31-day-long incubation period of barbtails (Greeney 2008a; this study) is the longest reported for any furnariid (Remsen 2003; Skutch 1996). Conversely, the incubation constancy of barbtails is lower than that reported for other furnariids (Skutch 1996).

While the adoption of contact incubation in birds is a highly conserved aspect of avian reproduction, the methods used by birds to care for their eggs vary tremendously in such aspects as participation of the sexes, incubation periods, and incubation rhythms (Deeming 2002c). When compared to other passerines, the daily percentage coverage provided by most furnariids (Skutch 1996) falls within the normal levels of diurnal adult attendance for passerines of a comparable size (approx. 75% according to Deeming 2002a). While the details of daily incubation patterns are lacking for most tropical species, data from several other passerines from northeastern Ecuador have provided preliminary comparisons (Fig. 6). A comparison of the rhythms of the Spotted Barbtail with those of two other enclosed-ball nesting species in the same family (White-Browed Spinetail, *Hellmayrea gularis* and the Andean Tit-Spinetail, *Leptasthenura andicola*) and two open-cup
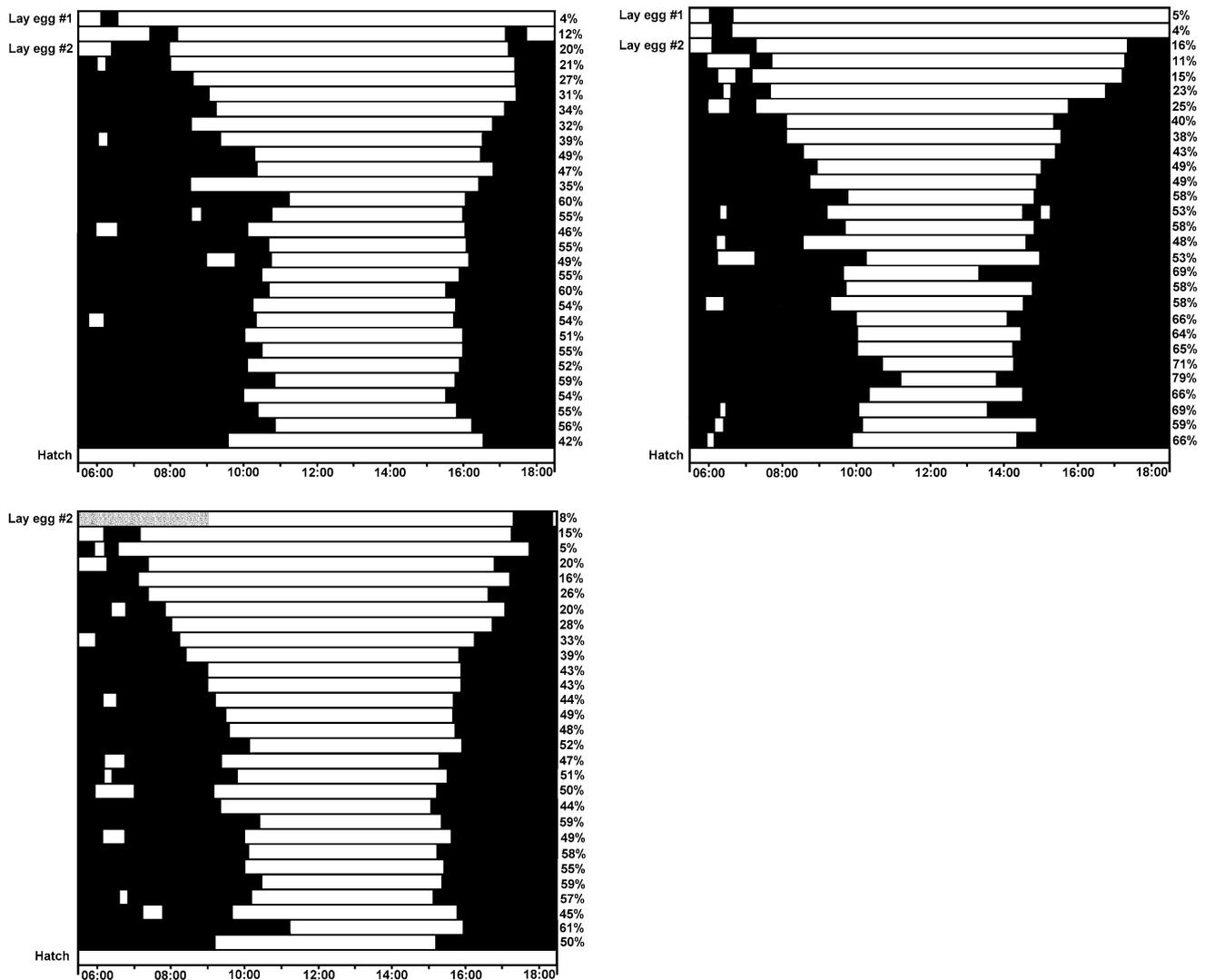
Figs. 2–4 Daily patterns of egg-coverage at three nests (Figs. **2**, **3**, **4**, respectively) of Spotted Barbtail that were both fitted with a probe below the inner surface of the nest lining to measure nest lining temperature and viewed with a video camera. Periods of adult presence in the nest are shown in *black*; *white areas* represent absences. Stage of incubation is shown on the *left*, and time of day is shown along the *bottom*. Total percentage coverage (0600–1800 hours) for each day is shown on the *right*

nesting ground-antbirds (Formicariidae: Tawny Antpitta, *Grallaria quitenesis* and the Peruvian Antpitta, *Grallaricula peruviana*) reveals that all six species are similar in having long periods of egg attendance (Greeney 2006; Greeney and Harms 2008; Greeney and Zyskowski 2008; HF Greeney, unpublished data). In contrast, the absence of adult barbtails for extended periods of times is strikingly different from behavior shown by other passerines in the area. The barbtails also show quite different diurnal rhythms from other, more distantly related species building enclosed nests along streams at the same elevation and in the same habitat as the barbtails (Dobbs and Greeney 2006; Greeney et al. 2006), such as the Streak-Necked Flycatcher (*Mionectes striaticollis*) and the Rufous-Breasted Flycatcher (*Leptopogon rufipectus*) (Fig. 6). Such comparisons

suggest that the unusual rhythms of egg attendance in barbtails are unlikely to be the result of phylogenetic constraints, nest form, or nesting habitat.

The interplay between numerous variables, including nest location and architecture, environmental conditions, egg size, clutch size, eggshell thickness, egg turning, and adult behavior affect the development rate of avian eggs (Deeming 2002a; Web 1987). For any given egg physiology and/or clutch size, the means by which a parent bird achieves the environmental conditions necessary for embryonic development involve both adult behavior and the physical characteristics of the nest and its location (Deeming 2002b; Hansell and Deeming 2002). This bird-nest unit not only provides developing embryos with the necessary microclimate (Ar and Sedis 2002), thereby
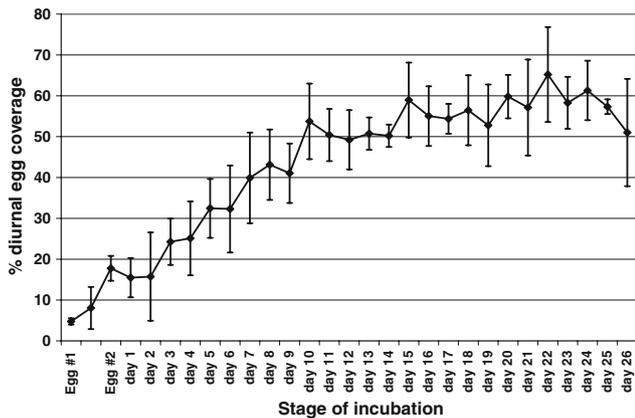
Fig. 5 Mean percentage diurnal (0600–1800 hours) attendance during incubation at three nests of Spotted Barbtail in northeastern Ecuador. *Error bars* show 1 SD. Percentage coverage is shown along the *y-axis*, and day of incubation is given along the *x-axis*

helping to maintain egg temperatures and control water loss, but also protects eggs from adverse weather, predators, and invasion by pathogenic bacteria (Cook et al. 2003; Hansell 2000; Thomson and Raveling 1987). The true extent to which the substantial walls of barbtail nests buffer the cool external climates of their nesting sites is unknown. However, the fact that internal nest temperatures drop to ambient during the long absences of adults, well below physiological zero (i.e., minimum temperature required for embryonic development is 25–27°C according to White and Kinney 1974), suggests that the parental absence seen here may be the reason for the extended incubation period of barbtails. The results of many prior studies relating the duration of on- and off-bouts during incubation with ambient temperature around the nest are equivocal (see references in Conway and Martin 2000a). Even with improved, non-linear regression models, we would expect a positive correlation with ambient temperature at temperatures below 26°C (Conway and Martin 2000a). While significance is low, the results reported here suggest a negative correlation between external temperature and off-bout duration in barbtails.

There is a significant correlation between total clutch mass and attentiveness across all avian species (Deeming 2002b). When separated into species with single-parent and dual-parent incubation, the correlation breaks down for dual-parent incubation and is significant only for species where parents do not share incubation duties (Deeming 2002b). Species with dual-parent incubation averaged over 90% attentiveness, with no correlation to clutch mass. Given a clutch size of two and a mean fresh egg weight of 3.5 g for barbtails (Greeney 2008a), we find that barbtails fall below the mean incubation attentiveness for comparable clutch masses, for species with dual- and with single-parent incubation, respectively. Based on Deeming's (2002b) sample of
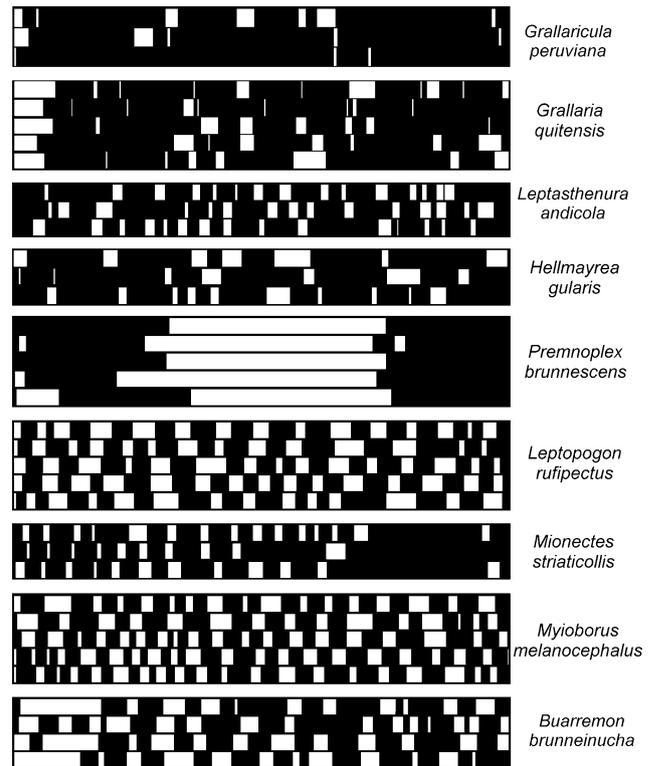

Fig. 6 Comparison of daily patterns of egg attendance in nine species of passerines nesting above 2000 m a.s.l. in northeastern Ecuador. The time period shown is from 0600 to 1800 hours each day, with each *horizontal column* representing a day. *Black portions* indicate adult presence at the nest and *white areas* show periods of absence. Data for each species were taken from the following sources: *Grallaricula peruviana* (Greeney 2006), *Grallaria quitensis* (Greeney and Harms 2008), *Leptasthenura andicola* (H.F. Greeney, unpublished), *Hellmayrea gularis* (Greeney and Zyskowski 2008), *Premnoplex brunnescens* (this study), *Leptopogon rufipectus* (H.F. Greeney, unpublished), *Mionectes striaticollis* (Greeney et al. 2006), *Myioborus melanocephalus* (Greeney et al. 2008), *Buarremon brunneinucha* (H.F. Greeney, unpublished)

354 species, 47% attentiveness to a clutch mass of 7 g is lower than that reported for any other species.

The number of trips adults make to and from a nest may directly impact their chance of detection by predators (Conway and Martin 2000b; Ghalambor and Martin 2000). Adults may even alter their rates of visitation in response to perceived increases in immediate predation risk, such as the visual detection of a potential predator (Ghalambor and Martin 2001, 2002). Thus, during incubation in high-predation risk species where one sex incubates, selection should favor longer on-bouts followed by longer off-bouts (Conway and Martin 2000b). Life-history theory predicts that species with higher rates of nest predation should evolve nesting strategies that minimize the duration of the nesting cycle and, consequently, the exposure of their offspring to predation (Bosque and Bosque 1995). Since long off-bouts may allow eggs to drop below temperatures where

embryonic development stops, extensive absences from the nest may hinder development and thus increase incubation period (Haftorn 1988; Williams 1991). To compensate for this conflict between selective pressures, a species such as the Spotted Barbtail, with dual-parent incubation, should adopt a strategy whereby adults replace each other infrequently but maintain a high level of incubation constancy. If barbtails are long-lived, however, they may reduce their effort during any individual reproductive event (Barbraud and Weimerskirch 2001), thereby decreasing offspring survivorship but avoiding energetic costs that may affect future reproduction (Visser and Lessells 2001). Similarly, long-lived species would be expected to adopt an incubation strategy that minimizes their own exposure to predators while at the nest. In the case of Red-necked Greebes, which show a similarly long period of egg-neglect (Nuechterlein and Buitron 2002), it is thought that adults abandon the nest during periods of high-predation risk (to themselves). Unfortunately, too little information is currently available on potential predators of barbtail nests, and it is unclear if mid-day is a period of high-risk for adults. In short, with little information available on the general ecology of barbtails, the explanations for their unusual incubation rhythms remain unclear.

As illustrated here (Fig. 6), the incubation rhythms of barbtails are irregular when compared to those of other passerines and even when compared to observations on a variety of species in the same family (Greeney and Zyskowski 2008; Skutch 1962, 1967, 1969, 1981, 1996). As described above, many variables may influence the evolution of incubation behavior, and these need further investigation before this attendance pattern can be fully understood. Larger sample sizes of closely studied nests are needed to elucidate the interactions between food availability, adult foraging strategies, ambient temperatures, predation risk, adult activity at the nest, and overall attentiveness. Comparative studies of the unknown incubation behaviors of phylogenetically and ecologically similar species of *Margarornis* tree runners (Irestedt et al. 2006; Remsen 2003) would be particularly informative. The broad geographical and altitudinal distribution of the Spotted Barbtail make this species an excellent study system for testing a variety of these hypotheses.

Zusammenfassung

Ungewöhnliche Bebrütungsrhythmen beim Westlichen Fleckenstachelschwanz (*Premnoplex brunnescens*)

Der westliche Fleckenstachelschwanz bewohnt das Unterholz humider Bergwälder in Mittel- und Südamerika. Abgesehen von grundlegenden Informationen über Eier und die Form des Nests ist wenig über seine Brutökologie veröffentlicht worden. Mittels Temperaturfühlern in Napfnestern zeige ich tägliche Muster der Bebrütung von drei Nestern in Ostecuador und decke einen bemerkenswerten Bebrütungsrhythmus auf. Nach nahezu konstanter Bebrütung am Morgen lassen die Altvögel die Eier für die meiste Zeit des Tages unbeaufsichtigt und kehren erst am späten Nachmittag zurück. Die mittlere Dauer (±SD) dieser Abwesenheit über die gesamte Bebrütungszeit der drei Nester betrug 6.4 ± 1.9 h. Ich diskutiere diese Ergebnisse im Hinblick auf ihre physiologische und ökologische Bedeutung.

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