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PREDATION, NEST ATTENDANCE, AND LONG INCUBATION PERIODS OF TWO NEOTROPICAL ANTBIRDS

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Abstract. Why do many tropical bird species have long incubation periods despite high risk of nest predation? Life history theory predicts that high predation should select for rapid developmental periods. A common explanation for this paradox is that parents reduce nest attentiveness to decrease the costs of parental effort, which lengthens incubation periods but also increases the chances for adults to have future reproductive opportunities. We evaluated the assumptions of that explanation and investigated an alternative hypothesis. That hypothesis says that parents should invest more as offspring value increases, and reduce investment when the chances of the investment paying off are low. When nest predation risk is higher early in incubation than later, parents can lower the costs of incubation to themselves by reducing nest attendance, but less attendance can lengthen incubation periods, which may expose eggs to greater mortality risk overall. We studied temporal patterns of nest predation and nest attendance by two species of Panamanian antbirds. Attentiveness was lowest the first six days of incubation, then increased as eggs aged. Nest predation, however, was six times greater during those first six days than later. We suggest that incubation periods are indeed lengthened by reduced parental attentiveness, but not just because parents may save the energetic costs of incubation or increase foraging time. Instead, inconstant time-dependent mortality risk to eggs (and possibly adults) at nests favors reduced attendance when risk is high and eggs are young. As eggs grow older and increase in value, parents invest more in their care. The savings in costs to parents should appear if predation risk is very high early in the incubation period. They can use the survival of eggs beyond an initial period of high risk to predict the greater likelihood of nest survival later, thus increasing the value of their own energetic investments later in the nesting cycle. *Accepted 3 September 2008.*

Key words: incubation, life-history evolution, nest attentiveness, nest predation, parental investment.

INTRODUCTION

High risk of nest predation is common among tropical birds (Ricklefs 1969, Robinson *et al.* 2000). Paradoxically, many tropical birds have long incubation periods even when predation is common and selection for rapid developmental periods would be expected (Ricklefs 1993, Bosque & Bosque 1995). One explanation for this paradox is that adults avoid elevating one key cost of reproduction, their own risk of mortality, by reducing the effort put into incuba-tion, thereby lengthening incubation periods (Ghalambor & Martin 2001, Martin 2002). Longer in-cubation periods can expose eggs to predation for more time, but may decrease adult mortality rate, thus permitting future breeding opportunities. That explanation assumes one or more of at least three factors that increase adult mortality risk during in-cubation: the energetic costs of incubation, loss of self-maintenance and foraging time while incubating, and higher risk of mortality to adults at the nest. We briefly summarize evidence for all three factors and find that an alternative solution is needed.

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Do tropical birds reduce breeding effort to keep their own mortality risk low?

Evidence demonstrating an increased mortality risk from the energetic costs of incubation in birds is equivocal (Thomson *et al.* 1998). Only a few studies have compared incubation metabolic rate (IMR) with resting metabolic rate (RMR) in passerines. Four of seven studies showed higher IMR than RMR, but none showed elevated mortality with higher IMR (Thomson *et al.* 1998). A study of great tits (*Parus major*) in Europe found a higher mortality of adults when clutch size was increased, but did not measure IMR (Visser & Lessels 2001). Furthermore, the four studies showing higher IMR were species breeding at northern latitudes where breeding birds experienced ambient temperatures outside their thermoneutral zone. No data exist for tropical species, many of which experience relatively limited ranges of ambient temperatures during breeding (Stratford & Robinson 2005). Therefore, insufficient data exist to support the idea that incubation imposes important energetic costs on tropical passerines.

Mortality rates (costs of incubation) might be elevated if incubating tropical birds lost valuable time for foraging or self-maintenance. Several lines of evidence indicate that food is probably not limiting during the breeding season for many species. Skutch (1985) argued that food must not be limiting because many breeding tropical birds spend more than half of each day loafing rather than foraging. Many lowland forest birds have lower-than-expected basal metabolic rates and engage in a "slower pace of life" (Ricklefs & Wikelski 2002, Tieleman *et al.* 2005). Few species in lowland rainforest carry visible fat stores, suggesting high predictability of food supplies (WDR, unpublished data). Finally, in pairs of north-temperate and subtropical congeners, eight Argentinian species had higher food delivery rates to nestlings than eight species in Arizona (Martin *et al.* 2000). Recent experiments show food-provisioning to adults during incubation may increase the time spent incubating eggs, but this increased incubation time does not always reduce incubation period (Chalfoun & Martin 2007). Currently available evidence aligns against the idea that incubation restricts access to food and causes elevated mortality.

Finally, parental effort put into incubation could be costly if parents are exposed to a greater risk of mortality when eggs are attacked by predators (Ghalambor & Martin 2001). Examples are known from waterfowl and parrotlets (Stoleson & Beissinger

2001), but data from songbird studies are rare (Magrath 1988). Below, we present data from Panamanian antbirds indicating that predation of adults at the nest is rare. Nevertheless, reducing nest attentiveness to lower the risks of death for the adults at the nest is a problematic argument. Presumably embryonic development in a species requires a certain minimum number of degree-hours, called the thermal dose. In fact, total incubation time may even increase if adults take so many recesses that eggs cool and must be repeatedly re-warmed (Boersma 1982). Therefore, adults cannot reduce the risk of their own mortality at the nest by reducing attentiveness because they cannot reduce the thermal dose required by embryos.

An alternative explanation for reduced nest attentiveness is provided by parental investment theory, which predicts that organisms should invest more in their offspring as the value of those offspring increases (Trivers 1972). Offspring value is an increasing function of offspring age (Ricklefs 1969, Dawkins & Carlyle 1976, Redondo 1989). If parents invest more in offspring of higher value, then nest attendance should increase with offspring age. In particular, if time-dependent mortality is inconstant across the nesting cycle and varies in a predictable manner, parents should reduce attendance when risk of nest loss is predictably high, unless nest attendance and defense can reduce the risk of nest loss. Nests that survive periods of high predation risk are then of higher value and worth increased levels of parental attendance. Reduced attendance during periods of higher risk could be a mechanism for lengthening incubation periods. We examined this hypothesis by quantifying time-dependent mortality and nest attentiveness across the developmental periods of Panamanian antbirds.

METHODS

We searched for nests of Chestnut-backed Antbirds (*Myrmeciza exsul*) and Spotted Antbirds (*Hylophylax naevioides*) between April and August 2000–2001, in the forest understory of Barro Colorado Island (BCI), Republic of Panama. BCI is a 1562-ha former hilltop, now isolated by the waters of Lake Gatun and the Panama Canal. The vegetation is classified as tropical moist forest, with approximately 2.6 m of rain falling per year (Windsor *et al.* 1990). The forest on the western half of the island, where we made our observations, is considered old-growth exceeding 400 years in age (Willis 1974, Robinson 1999).
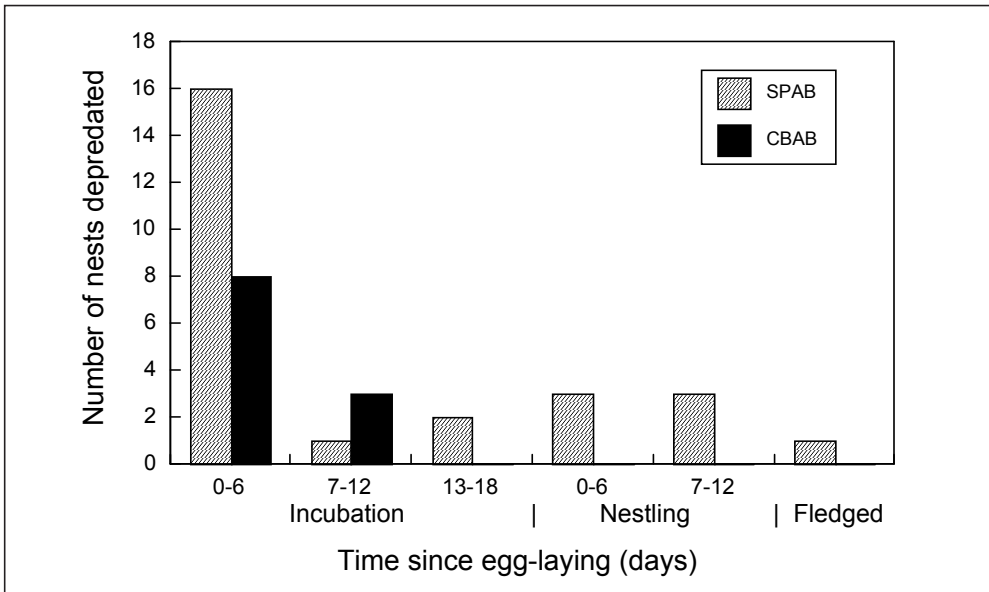
FIG. 1. Number of nests lost to predators declined with time after onset of egg-laying. Data are presented in 6-day intervals. One of 26 Spotted Antbird (SPAB) nests discovered during construction fledged young. None of 11 Chestnut-backed Antbird (CBAB) nests fledged young.

Both Chestnut-backed Antbird and Spotted Antbird typically lay two-egg clutches and have incubation periods of 16 and 18 days, respectively (Willis 1972, Willis & Oniki 1972). All nests were found and monitored following methods described in Robinson *et al.* (2000). We studied Chestnut-backed and Spotted Antbirds because they are common on BCI (Robinson 2001) and their nests are placed in the forest understory. Chestnut-backed Antbirds place their open-cup nests on the ground (Willis & Oniki 1972). Spotted Antbirds weave an open-cup nest into a branch of a small sapling one meter above ground (Willis 1972).

Predation risk. We measured nest predation on BCI and in the closest mainland forest (250 m from BCI). Nest failure did not differ consistently between BCI and the mainland (WDR & GR, unpublished) so we combined data for evaluations of temporal patterns of predation. Only nests found during construction were included in temporal pattern analyses. We compared with a contingency test the observed failures with those expected if nest predation occurred with equal frequency across five 6-day intervals during the nesting period.

Video monitoring. We used three miniature video-camera systems (Fuhrman Diversified, Inc., Seabrook, Texas) to continuously observe nests and record data, using a similar method as described by Thompson *et al.* (1999) and Robinson *et al.* (2005). Since each recorder was located 15 to 18 m away from nests, we did not visit nests each day unless an absence of bird activity suggested nest failure.

For each 24-h period we noted: number of eggs or nestlings present, time spent incubating or brooding by each parent, duration of recesses from incubation and brooding by each parent and time nest was unattended by both parents, number of feeding trips by each parent, and identity of predators visiting nests.

RESULTS

Predation risk. We monitored 32 Chestnut-backed Antbird (CBAB) and 53 Spotted Antbird (SPAB) nests. Of those, 11 CBAB and 26 SPAB nests were found during nest construction. Seventy-three percent of CBAB and 61% of SPAB nests were depredated in the first six days after egg-laying began (Fig. 1). Risk of nest failure was inconstant with

respect to time for SPAB (χ^2 = 10.7, df = 4, P = 0.029; CBAB N too small for comparison). All predation was diurnal.

Nest attentiveness. We video-monitored 6 CBAB and 7 SPAB nests. Despite biparental care, clutches were left unattended much of the day during incubation. CBAB nests were incubated 40%, and SPAB nests 65% of each day when averaged across the entire incubation period (Table 1). Males incubated more than females during daytime (CBAB: U = 3.0, P = 0.008, N = 6; SPAB: U = 6.0, P = 0.009, N = 7). Male CBAB averaged 32.1% (SE = 8.5) of each day incubating, whereas females averaged 10.4% (SE = 4.9). Male SPAB also incubated more (mean = 40.1%, SE = 4.6) than female SPAB (mean = 25.0%, SE = 3.2). Nocturnal incubation was common, even during the first 6 days after egg-laying, and was done exclusively by females (Table 1).

Attendance at nests increased strongly as incubation progressed (Fig. 2). For example, observation sequences from CBAB indicated that percentage of each day spent incubating after clutch completion increased from 6% in the first 3 days of the incubation period to 76% later, and from 27% to 86% in SPAB. All nests showed a similar pattern (Fig. 2). The longest sequences of observations also showed that adults relieved each other more often toward the end of the incubation period, thus incubation bouts were significantly shorter (r = 0.79, P < 0.005 for CBAB, and r = 0.76, P < 0.005 for SPAB).

Adult mortality and nest defense. We observed no evidence of adult mortality at nests during incubation or nestling periods. During a nest predation event, defense by adults appeared to be ineffective and of low risk. Cameras detected ten predation events. Eight were by snakes (*Pseustes peocilonotus*, one by a capuchin monkey (*Cebus capucinus*) and one by a coati (*Nasua narica*) (Robinson *et al.* 2005). Adults defended against four snakes and unsuccessfully thwarted predation each time. No adult mortality was observed during defense.

DISCUSSION

Our data show strong temporal variation in the risk of nest mortality as incubation proceeded. Most nests were lost to predators within the first six days after egg-laying began. During those first six days, adults of both antbird species spent relatively little time at nests. Incubation time gradually increased from late in the first week to the third week as hatch dates approached. The patterns we observed at nests of these two antbird species are consistent with predictions of parental investment theory if nest attendance

TABLE 1. Time (mean percent min/d ± SE) spent incubating and recessing from incubation by each sex at nests of Chestnut-backed Antbirds (CBAB) and Spotted Antbirds (SPAB) on Barro Colorado Island, Panama. Recesses are the complement of incubation. The number of nights header represents the quantity of nights the female incubated vs. the total number of nights monitored by video.

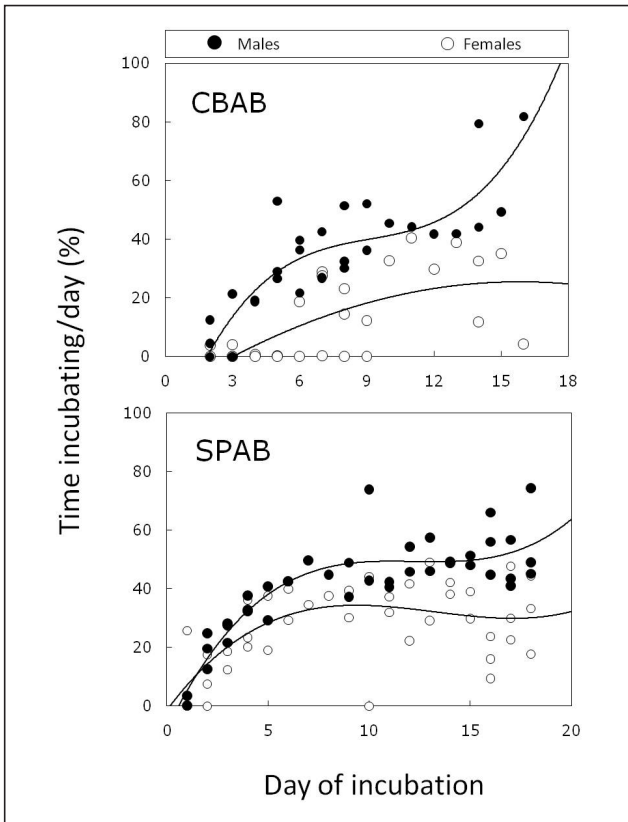| Species	Nest number	Incubation males	Incubation females	Number of nights	Egg age range (d)
CBAB	1	4.5 ± 0.0	3.8 ± 0.0	0/1	1-3
	2	26.4 ± 3.2	10.8 ± 4.6	3/6	1-8
	3	31 ± 10.9	0.04 ± 0.02	0/7	1-8
	4	29.5 ± 0.0	0	0/0	2
	5	38 ± 3.3	24.4 ± 4.9	8/9	3-14
	6	63.2 ± 12.6	23.2 ± 11.4	2/2	14-16
SPAB	1	49 ± 12.4	18.5 ± 4.7	2/2	14-16
	2	53.3 ± 2.6	28.9 ± 2.6	8/8	9-17
	3	44.5 ± 18.3	24.1 ± 15.1	3/3	7-10
	4	39.2 ± 3.2	34.5 ± 3.1	14/17	1-18
	5	43.1 ± 4.6	34.6 ± 4.6	13/13	5-18
	6	31.4 ± 6.5	18.4 ± 4.5	3/5	1-5
	7	20.1 ± 7.0	16.2 ± 3.9	2/2	1-3

FIG. 2. Percentage of time spent incubating per day by males and females of Chestnut-backed Antbirds (CBAB) and Spotted Antbirds (SPAB) from onset of incubation until hatching. Nocturnal incubation by females is excluded. Fitted lines are cubic regressions: CBAB males ($y = 0.08x^3 - 2.16x^2 + 21.08x - 32.42$, $r^2 = 0.74$), CBAB females ($y = -0.16x^2 + 4.93x - 13.56$, $r^2 = 0.44$), SPAB males ($y = 0.03x^3 - 1.18x^2 + 14.31x - 7.85$, $r^2 = 0.76$), SPAB females ($y = 0.02x^3 - 0.77x^2 + 9.29x - 1.36$, $r^2 = 0.31$).

is positively correlated with investment by parents in offspring care.

Compared to most temperate passerines, where leaving a clutch unattended for more than 25% of a day (even when incubation is by only one parent) is less common (Deeming 2002), antbirds appeared almost to ignore their nests for the first week when most nests were lost to predators. Leaving nests unattended during periods of high risk suggests that birds may use that time to assess the relative safety of their nest site. If nests survive past the first week, then the contents are more worthy of continued investment. Field experiments demonstrate that some birds can evaluate relative predation risk (Fontaine & Martin 2006). In environments where risk of nest loss is high, selection could favor parental strategies that reduce breeding effort until investment pay-offs are predictably greater. Birds may be unable to predict which particular nest sites are safer when they

are selecting sites and building nests, but could use nest survival through the first week as a predictor of greater likelihood of eventual success, and therefore greater value of those nests. Furthermore, costs of reduced early attendance, such as decreased embryonic viability in eggs, could be mitigated by nocturnal incubation. Rarity of nocturnal predation events may allow incubating females to maintain egg viability during that risky first week. Many studies document reduced embryonic growth when eggs are unattended for a few hours, or days, by cooling, greater microbial growth, or both (Boersma 1982, Cook *et al.* 2005). In the warm understory of the lowland tropics, eggs may not require as much incubation early on, especially during the day (Beissinger *et al.* 2005), to maintain viability.

Our results support the idea that nest predation drives the response in nesting behavior, since parental activity at the nest does not positively correlate

with higher risk of predation (e.g., higher replacement rate toward hatching date). Components of our solution overlap with previous explanations. Opportunities for foraging and self-maintenance may still play a role. If predation occurs significantly more often early in the incubation period, adults may opt at that time to continue foraging for self-maintenance rather than spend time incubating, so that re-nesting is less energetically taxing. The higher attendance during daytime by males than by females is consistent with the hypothesis that females may be foraging to recover or maintain energy levels after egg-laying. Females lose no foraging time by incubating at night. In this way, parents are avoiding some costs of parental effort, but no data exist to evaluate any additional risk to adult mortality if parents incubated eggs instead. In a landscape where some pairs initiate as many as 13 nests per breeding season (Willis 1974), such an energy-conserving approach could be favored. In contrast, another potential risk factor, the chance of an adult being killed at the nest, appeared to be very low. Adult mortality at the nest was observed only twice in observations of more than 600 nests of SPAB and CBAB in forests near BCI (Robinson *et al.* 2000, Styrsky 2003).

We do not yet know if the lower nest attendance we observed in the first week actually lengthens incubation periods. Since none of the birds we observed had high attendance in the first week, we cannot compare incubation periods of birds with high and low early attendance. Experiments taking fresh eggs and placing them in incubators under conditions simulating constant nest attendance could quantify how much shorter antbird incubation periods could be. An experiment with Panamanian House Wren (*Troglodytes aedon*) eggs showed that incubation periods of eggs in incubators were not shorter than those of eggs in natural nests (Robinson *et al.* 2008). Furthermore, the quantitative costs of lengthening incubation periods by up to a few days could be modeled and compared against the anticipated benefits to parents of reducing investment in risky nests. Obtaining field measurements of the benefits, such as increased time for foraging and recovery from egg-laying, however, will be challenging.

In summary, if inconstant time-dependent mortality of eggs, and increasing nest attentiveness as eggs age, turn out to be widespread in tropical birds, then parental investment decisions provide an alternative explanation for longer incubation periods of tropical birds than previous explanations.

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