

JUVENILE MORTALITY INCREASES WITH CLUTCH SIZE IN A NEOTROPICAL BIRD

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Abstract. The change in avian clutch size with latitude is a celebrated example of geographic variation in a vertebrate life-history trait. Alternative hypotheses for this pattern invoke nest predation, limited food for nestlings, or post-fledging juvenile mortality as selection pressures leading to small clutch size of tropical birds. We manipulated the clutch size of Spotted Antbirds (*Hylophylax naevioides*) in central Panama to test these hypotheses. We observed that rates of nest predation were not influenced by parental activity at nests and parents could successfully feed nestlings in enlarged broods. Although larger broods produced the most fledged juveniles, these individuals were less likely to survive to dispersal than were juveniles that fledged from smaller broods. Consequently, nest productivity did not vary with clutch size. Post-fledging mortality was not related to nestling mass two to three days prior to fledging. Rather, differences in the allocation of parental investment per juvenile among differently sized broods appeared to influence juvenile survival probability. These results identify parental care during the post-fledging period as a potential key factor influencing the evolution of small clutch size in tropical birds.

Key words: clutch manipulation; clutch size; food limitation; *Hylophylax naevioides*; juvenile mortality; life history; Neotropics; nest predation; parental care; post-fledging; Spotted Antbird.

INTRODUCTION

One of the most striking examples of geographic variation in a life-history trait is the change in avian clutch size with latitude (Moreau 1944, Lack 1947, 1948, Cardillo 2002). Birds breeding at tropical latitudes produce significantly smaller clutches than those breeding in north temperate regions (Moreau 1944, Ricklefs 1969, Skutch 1985, Yom-Tov et al. 1994), a pattern that persists after accounting for phylogeny (Martin et al. 2000, Cardillo 2002). Within tropical regions, a clutch size of two eggs is nearly universal for an ecologically and taxonomically diverse suite of species (Skutch 1985). The selective pressures leading to this comparatively small and consistent clutch size have been debated for over 50 years (Martin 1996).

Two dominant hypotheses for small clutch size in tropical birds involve food limitation and nest predation. The food limitation hypothesis posits that females lay the number of eggs that maximize the number of young they can rear successfully, which is determined by food supply available to nestlings. By extension, scarcity of food in tropical habitats limits clutch size in these regions (Lack 1947). An alternative hypothesis

is that the most productive clutch size is a function of nest predation if an increase in rates of food delivery to larger broods attracts more predators to the nest (Skutch 1949, 1985). High rates of nest predation may also select for small clutch size to reduce the investment in any single nest attempt (Slagsvold 1982, 1984, Martin 1995). Nest predation rather than food supply likely has a stronger influence on avian life-history evolution (Martin 1995), although a comparative study of birds breeding at northern and southern latitudes has shown that nest predation explains variation in clutch size within, but not between geographical regions (Martin et al. 2000). Direct experimental tests of these hypotheses in tropical habitats are lacking.

The food limitation and nest predation hypotheses assume that selective pressures during the nestling period determine clutch size. The post-fledging period, however, may be the more critical stage of reproduction for tropical birds (Karr et al. 1990, Russell 2000). Relative to north temperate species, many tropical and south temperate birds continue to feed and defend fledged juveniles for an extended period after they leave the nest (Ricklefs 1969, Fogden 1972, Russell 2000). An inverse relationship between clutch size and duration of post-fledging parental care has been noted along elevational gradients in temperate regions and likely represents a trade-off between offspring number and quality (Badyaev and Ghalambor 2001). Moreover, because of high rates of nest predation, the reproductive value of fledged juveniles in tropical regions may be

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higher than that of eggs or nestlings (Ricklefs 1969). Within tropical regions, if offspring survival is increased by extended post-fledging parental care, then greater parental investment in fewer juveniles may significantly enhance fitness (Fogden 1972, Karr et al. 1990, Martin 1996).

We manipulated clutch size of Spotted Antbirds (*Hypothymalys naevioides*) to assess the relative importance of nest predation, nestling food limitation, and post-fledging juvenile mortality as alternate selection pressures influencing clutch size. This species typifies the tropical life-history pattern, with a small clutch of two eggs and an extended two-month period of post-fledging parental care (Willis 1972, Styrsky 2003). If predation rates are influenced by adult activity at the nest, we predicted that adults would make more trips to feed larger broods and, consequently, these broods would experience higher rates of nest predation relative to smaller broods. If ability of parents to provision nestlings limits clutch size, we predicted a lower per-nestling feeding rate for larger broods, resulting in reduced nestling mass and fewer fledged juveniles compared to smaller broods. Finally, if the effectiveness of post-fledging parental care is inversely related to brood size, we predicted that juveniles from larger broods would be the least likely to survive to natal dispersal.

METHODS

We conducted this clutch-size manipulation from 1999 to 2001 in Parque Nacional Soberanía, a 22 000-ha lowland, tropical moist forest in the Republic of Panama. Our study site was within the Limbo Basin (9°9'35" N, 79°44'36" W; see Karr [1971] and Robinson et al. [2000] for a detailed description of the study site). The focal species for this research was the Spotted Antbird, a nonmigratory insectivore endemic to the Neotropics. In central Panama, Spotted Antbirds breed during the wet season, from April through late September (Willis 1972, Styrsky 2003). Nests are open-cup structures placed in saplings in the forest understory (Willis 1972). Spotted Antbirds characteristically lay a clutch of two eggs but occasionally will produce a clutch of one egg (5.18% of nest attempts in this study population [$n = 328$]; Styrsky 2003). Clutches of three eggs have never been reported.

We randomly assigned clutches initiated within 24 h of each other to different experimental treatments and then transferred eggs between these nests to create reduced clutches of one egg ($n = 45$) and enlarged clutches of three eggs ($n = 40$). Control nests contained two eggs ($n = 170$) and were found at the same stage of development as nests in the experimental treatments, but were not initiated within 24 h of any other nest in the study population. Consequently, we could not transfer same-age eggs between these control nests. Because the purpose of this manipulation was to generate broods with different numbers of nestlings, non-manipulated nests in which only one egg was laid ($n = 13$), only

one egg hatched ($n = 10$), or brood size was reduced naturally ($n = 4$) also were included in the reduced-clutch treatment. These natural one-egg clutches and broods were distributed among 19 females, all of which regularly produced two-egg clutches during the years of this study.

Eggs were collected or moved between nests within one day after the second egg in the clutch was laid. No experimental nests were abandoned in response to either the clutch reduction or enlargement treatments. All transferred eggs that were not depredated during the incubation stage hatched successfully, indicating that Spotted Antbirds are capable of incubating a clutch of three eggs and that the clutch manipulation did not decrease egg viability. All nests were monitored every three days until the nestlings fledged or the nest was depredated.

Nest visitation rates by adults were estimated at all nests with nestlings in all years of the study. Each nest was observed up to three times during the nestling stage. The first observation occurred on brood day 2–4, the second on brood day 5–7 (2000–2001 only), and the third on brood day 8–10. Most observations (93%, $n = 163$) were initiated between 06:45–09:15 Eastern Standard Time (EST), and the mean onset was at 07:58 ± 48 min. Visitation rate was not related to the time of day these nests were observed ($r^2 = 0.002$, $df = 162$, $P = 0.561$, reciprocally transformed data). Each observation period lasted for one hour, and visitation rate was calculated as the total number of adult arrivals to a nest per hour. We estimated the amount of food brought to the nest whenever possible, although often our view of the adult's bill was obstructed. Data from all observations of multiple nests of the same pair of birds ($n = 15$ pairs) were averaged so that each pair was represented only once in a given treatment.

We marked each breeding adult and nestling with a unique combination of a numbered aluminum and three colored-plastic leg bands. Adults were captured on their territory using mist nets and playback tapes of conspecific songs and calls. Nestlings were banded and weighed on brood day 8 or 9. Nests were checked one day prior to fledging (brood day 10) and on the date of fledging to verify that fledging occurred. We searched each territory for fledged juveniles (or for the adult pair if the nest had been depredated) within 24 h of the final check to confirm nest fate. Adults with fledged juveniles always gave alarm calls in response to our presence, whereas adults whose nest had been depredated did not alarm call and almost always were observed courtship feeding or making courtship calls to one another (J. N. Styrsky, unpublished data).

We assessed post-fledging survival by repeatedly re-sighting marked juveniles on their natal territory for up to 50 days post-fledging. Re-sighting effort was similar among treatment groups. During the first 14 days post-fledging, we attempted to re-sight juveniles every three days, and thereafter once a week either until they

dispersed or until the end of each field season. If we did not locate any juveniles on a particular visit to a territory, we returned the following day to search that territory, and thereafter every two to three days until either juveniles or a replacement clutch were located. After identifying individual juveniles, we recorded the number and identity of adults attending each juvenile and quantified adult alarm calls and juvenile-provisioning behaviors.

Juvenile birds that disappeared within 28 days after fledging likely died on their natal territories. Juvenile Spotted Antbirds do not reach adult size and tail length until 21 days post-fledging, do not begin to forage independently until 28 days post-fledging, and are fed regularly by their parents for over 35 days post-fledging (Willis 1972). Thus, juveniles younger than 28 days of age are physiologically and developmentally incapable of surviving on their own without parental care. Most (98%, $n = 44$) juvenile disappearances, in fact, occurred well before 28 days post-fledging (see *Results*). Around 30 days of age, juveniles call repeatedly to their parents and thus are not easily overlooked as they mature (Willis 1972; J. N. Styrsky, *unpublished data*). We never re-sighted juveniles that disappeared during the first 28 days out of the nest, even though we continued to search the territory and surrounding areas for up to 50 days post-fledging, when natal dispersal usually begins (Willis 1972; J. N. Styrsky, *unpublished data*). Furthermore, pairs that lost all juveniles from a brood would immediately initiate courtship behaviors in preparation for a new nest attempt, whereas pairs with surviving juveniles did not initiate new nest attempts until at least a month after their previous nest had fledged (Styrsky 2003). This marked difference in the behavior of parents in response to the presence or absence of fledged juveniles provided additional confirmation of juvenile survival status. We assumed any juvenile that disappeared from its natal territory after reaching nutritional independence had dispersed based on these patterns.

Statistical analyses

Nest visitation rates.—We tested for differences in visitation rates among treatments and among nestling age categories with a general linear model procedure (Proc Mixed; SAS Institute 1999). Because most nests were observed for more than one stage of nestling development, nest identity was treated as a repeated-class variable in this model. We also tested for differences between the control group and each experimental treatment with a series of post hoc pairwise comparisons, using sequential Bonferroni corrections to adjust for error. Nest visitation rates did not differ among years at any nestling age (2–4 days, $F_{2,52} = 0.41$, $P = 0.664$; 5–7 days, $F_{2,32} = 0.43$, $P = 0.654$; 8–10 days, $F_{2,32} = 0.73$, $P = 0.491$); thus, data from all three years were combined for this analysis.

Nest predation rates.—The daily predation rate was calculated as the total number of nest predation events divided by the total number of days that nests were exposed to predators during the nestling stage (Mayfield 1975). We compared differences in daily predation rates among treatments using the program CONTRAST (Hines and Sauer 1989). Because nest predation occurs at random with respect to nest site within this population of Spotted Antbirds (Styrsky 2005), we considered each nest attempt to be an independent unit of replication. Daily predation rates during the nestling stage did not differ within any breeding season (Styrsky 2003) nor among years ($\chi^2 = 0.174$, $df = 2$, $P = 0.917$), so data from all three years were combined.

Nestling mass.—We tested for differences in nestling mass among treatments using a general linear model procedure (Proc Mixed; SAS Institute 1999) in which identities of broods and breeding pairs were treated as random effects. We also used this procedure to test if nestling mass differed between juveniles that did or did not survive to dispersal. We also tested for differences in nestling mass between the control group and each experimental treatment with a series of post hoc pairwise comparisons, using sequential Bonferroni corrections to adjust for error. Data from all three years, along with additional nestling morphology and juvenile survival data that we collected at this study site in 1998, were combined for these analyses. Nestling mass did not differ significantly among years when age of measurement was controlled (main effect of year, $F_{3,74} = 0.60$, $P = 0.616$).

Fecundity of successful nests and post-fledging juvenile survival.—We used Kruskal-Wallis tests to determine if the number of juveniles that fledged from successful nests and the proportion of juveniles that survived to dispersal differed among treatments. Data from 1999 to 2001 were combined for the analysis of nest fecundity. For the analysis of post-fledging juvenile survival, results from all three years, plus additional data from 1998, were pooled. We estimated confidence intervals (95%) of mean post-fledging survival rates using a bootstrap resampling procedure (Systat 2004). Values from each treatment category for each week during the post-fledging period were resampled 500 times.

Overall productivity.—We used a Kruskal-Wallis test to determine if the number of juveniles per clutch that survived from egg laying to dispersal differed among treatments. For this analysis, nonexperimental nests in which only one egg was laid were included in the reduced-clutch treatment. Nonexperimental nests in which two eggs were laid but natural brood reduction occurred were treated as controls. Data from 1999 to 2001 were combined.

RESULTS

During the nestling period, rates of nest visitation differed significantly with brood size ($F_{2,55} = 33.73$, P

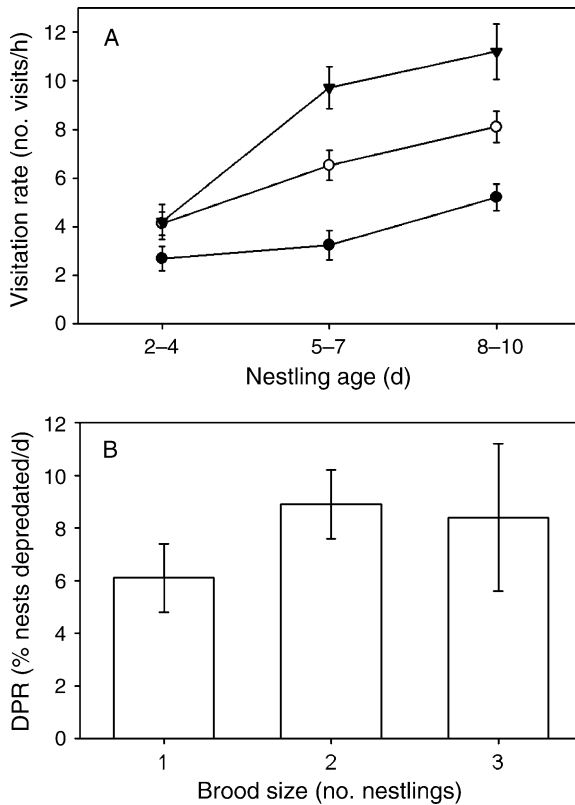


FIG. 1. (A) Nest visitation rate (mean \pm SE) by adult pairs to experimental nests with one (reduced broods, solid circles), two (control broods, open circles), or three (enlarged broods, triangles) nestlings. Sample sizes for each nestling age category (youngest to oldest) in each treatment: reduced broods, $n = 21, 15,$ and 18 ; control broods, $n = 24, 14,$ and 12 ; enlarged broods, $n = 10, 7,$ and 4 . Sample sizes vary with age category because of losses to predators and missed observations. (B) Daily predation rate (DPR; mean \pm SE) at experimental nests during the nestling stage. Sample sizes for each treatment: reduced broods, $n = 39$; control broods, $n = 69$; enlarged broods, $n = 13$.

< 0.0001) and with nestling age ($F_{2,61} = 32.84, P < 0.0001$). Adults visited reduced broods less frequently than control broods at all nestling age classes (age 1, $t = -2.11, P = 0.025$; age 2, $t = -3.84, P = 0.0003$; age 3, $t = -3.42, P = 0.001$; Fig. 1A). At the youngest nestling age category, adults visited enlarged broods as frequently as control broods (age 1, $t = -0.07, P = 0.947$), but then visited enlarged broods more frequently than control broods as nestlings aged (age 2, $t = -2.98, P = 0.004$; age 3, $t = -2.35, P = 0.022$; Fig. 1A). Despite this variation in adult activity at the nest, rates of nest predation did not differ significantly among treatments ($\chi^2 = 2.408, df = 2, P = 0.300$; Fig. 1B). Furthermore, nest predation rates did not differ between reduced and control broods ($\chi^2 = 2.335, df = 1, P = 0.127$), nor between control and enlarged broods ($\chi^2 = 0.029, df = 1, P = 0.865$).

Overall, adult visitation rate per nestling decreased marginally with brood size ($F_{2,55} = 2.87, P = 0.065$;

Fig. 2A). When each experimental group was compared to the control, however, per-nestling visitation rate did not differ between reduced and control broods (age 1, $t = 1.30, P = 0.198$; age 2, $t = -0.04, P = 0.968$; age 3, $t = 1.66, P = 0.103$), nor between control and enlarged broods (age 1, $t = 1.15, P = 0.253$; age 2, $t = 0.03, P = 0.975$; age 3, $t = 0.57, P = 0.568$). We lacked sufficient data to quantify the amount of food brought to the nest per visit, but never observed adults in any treatment group carrying more than one food item at a time. Consequently, Spotted Antbirds do not appear to alter their food delivery strategy in response to a change in brood size.

Controlling for age of measurement, nestling mass decreased significantly with brood size overall ($F_{2,50} = 3.20, P = 0.049$). Nestling mass was the same for reduced and control broods (day 8, $t = 0.51, P = 0.611$; day 9, $t = 1.09, P = 0.281$), but nestlings from enlarged broods weighed marginally less than nestlings from

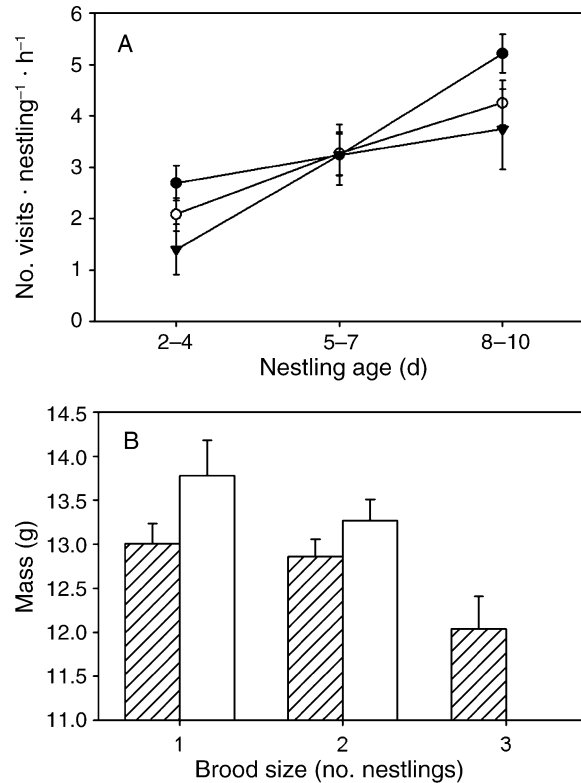


FIG. 2. (A) Per-nestling visitation rate (mean \pm SE) by adult pairs to experimental nests with one (solid circles), two (open circles), or three (triangles) nestlings. Sample sizes for each nestling age category (youngest to oldest) in each treatment: reduced broods, $n = 21, 15,$ and 18 ; control broods, $n = 24, 14,$ and 12 ; enlarged broods, $n = 10, 7,$ and 4 . (B) Nestling mass (mean \pm SE) measured on brood day 8 (hatched bars) or on brood day 9 (white bars). Sample sizes equal the number of independent adult pairs with broods included in each treatment: reduced broods, day 8, $n = 16$; day 9, $n = 6$; control broods, day 8, $n = 20$; day 9, $n = 9$; enlarged broods, day 8, $n = 6$; day 9, $n = 0$.

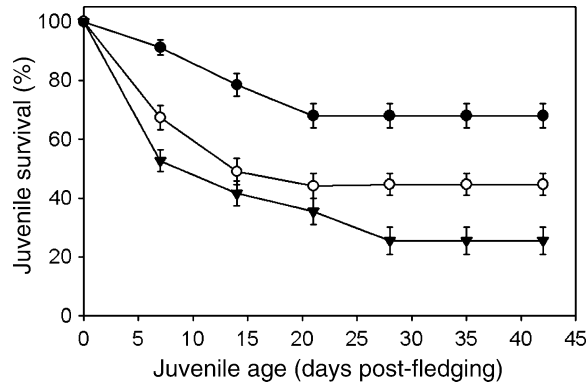


FIG. 3. The percentage of surviving juveniles from reduced (solid circles), control (open circles), and enlarged (triangles) broods plotted against number of days after leaving the nest (day 0 = fledge date). Sample sizes for each treatment: reduced broods, $n = 22$; control broods, $n = 24$; enlarged broods, $n = 5$. Error bars represent 95% confidence intervals.

control broods (day 8, $t = 1.96$, $P = 0.055$; Fig. 2B). Nestling mass, however, did not vary between the group of juveniles that survived the post-fledging period ($n = 37$) and the group that died prior to dispersal ($n = 44$; $F_{1,30} = 0.77$, $P = 0.387$).

Larger broods resulted in more fledged juveniles (reduced broods, 1.0 ± 0 [means \pm SE], $n = 17$; control broods, 1.92 ± 0.06 , $n = 24$; enlarged broods, 3.0 ± 0 , $n = 5$; $\chi^2 = 39.780$, $df = 2$, $P < 0.0001$). Because partial brood loss was rare in this study, the number of juveniles that fledged from successful nests was effectively equal to clutch size.

In contrast, juvenile survival rates during the post-fledging period were inversely related to brood size ($\chi^2 = 6.258$, $df = 2$, $P = 0.044$; Fig. 3). Solitary juveniles had a nearly 200% greater chance of surviving to dispersal than did juveniles with two siblings. Solitary juveniles were also more likely to survive to dispersal than were juveniles from control broods with one sibling ($\chi^2 = 4.071$, $df = 1$, $P = 0.044$). Although the 95% confidence intervals of mean post-fledging survival did not overlap as juveniles aged (Fig. 3), the proportion of juveniles surviving to dispersal did not differ between control and enlarged broods ($\chi^2 = 0.608$, $df = 1$, $P = 0.436$). Because of the small sample of enlarged broods, however, the power to detect a difference between the enlarged and control treatments was low. Over 70% of all juvenile deaths ($n = 44$) occurred in the first week after fledging, with 97.7% of all mortality occurring during the first three weeks post-fledging.

We observed four out of five enlarged broods on the day of fledging. In all cases, one adult immediately assumed sole care of the first juvenile that fledged while the second adult fed the two remaining juveniles in the nest. This second adult continued to divide care between the second and third juveniles even after one had

fledged and the other was still in the nest. All juveniles from enlarged broods fledged successfully within several hours of each other, but at least one juvenile from every enlarged brood died within the first few days of the post-fledging period.

Adults also divided the care of juveniles from control broods after fledging. In all observation periods ($n = 74$) of broods with two juveniles ($n = 19$) conducted during the first three weeks after fledging, we observed only one adult (and always the same individual) caring for each particular juvenile. In the majority of these observation periods ($n = 74$, 62%), we did not detect the second adult and juvenile even in the same general area of the territory.

In contrast, the single juvenile from reduced broods received care from both adults during the post-fledging period. In the first three weeks post-fledging, we recorded parental investment in broods of one juvenile ($n = 23$) on 97 different occasions (four observation bouts per brood). In the majority of these bouts (70%), both adults were observed tending the single juvenile; however, both adults were not providing the same level of care. Whereas both adults gave alarm calls in 95% of broods with one juvenile, a second adult provided food to the juvenile in only 32% of these broods.

Despite the low post-fledging survival of juveniles from larger broods, more juveniles fledged from these broods than from the other two treatment groups. Consequently, the average number of juveniles from each clutch of eggs that survived to dispersal did not differ among treatments (mean number of dispersing juveniles per clutch: reduced broods, 0.16 ± 0.05 , $n = 58$; control broods, 0.13 ± 0.03 , $n = 175$; enlarged broods, 0.10 ± 0.06 , $n = 40$; $\chi^2 = 1.945$, $df = 2$, $P = 0.378$).

DISCUSSION

In this study, the probability of nest predation was unrelated to brood size. Nest visitation rates did increase with brood size when adults were feeding nestlings; however, this increase in adult activity had no effect on nest predation rates. Our results, therefore, refute the nest predation hypothesis proposed by Skutch (1949, 1985) that tropical birds produce a small clutch to reduce adult activity at the nest and thereby minimize nest predation risk.

Our results also do not support the hypothesis that clutch size is limited by food availability to nestlings. As nestlings developed, parents were able to increase their feeding rate to larger broods so that nestling starvation was rare in all years of this study (2.2%, $n = 232$). Nestling starvation never occurred in enlarged broods, even in an exceptionally dry year (in 2001, with an annual rainfall of 1772.9 mm, when mean annual rainfall = 2592.4 mm) when food resources (i.e., leaf litter arthropods) likely were scarce (Levings and Windsor 1982). Consequently, larger broods produced the most fledged juveniles.

After fledging, however, juveniles from larger broods were less likely to survive to dispersal than were juveniles from smaller broods. Notably, this difference in post-fledging survival also occurred between the two brood sizes (one and two juveniles) naturally produced by Spotted Antbirds. One explanation for the inverse association between brood size and rates of post-fledging juvenile survival is that inadequate nourishment during the nestling period increases the risk of mortality soon after fledging. Nestling mass two to three days prior to fledging, however, was not associated with juvenile survival to natal dispersal. Furthermore, nestlings from control and reduced broods weighed the same, but experienced very different post-fledging survival rates. At fledging, Spotted Antbirds weigh only 75% of their adult body mass (Willis 1972); consequently, mass gains during the early post-fledging period rather than during the nestling period may have had a greater influence on survival. Other components of nestling condition (e.g., immunocompetence) also may have influenced later post-fledging survival and warrant further study.

Alternatively, juvenile survival in enlarged broods may be reduced by constraints on parental care during the post-fledging period. After fledging, adult Spotted Antbirds normally divide broods of two juveniles and each adult provides exclusive care to one juvenile, often on different parts of the territory (Willis 1972; J. N. Styrsky, *personal observation*). In contrast, when brood size was enlarged, one adult attempted to care for two juveniles without assistance, while the second adult provided care to the third juvenile. When brood size was experimentally reduced, both adults provided care to the single juvenile, although the second adult contributed primarily to increased vigilance against predators (i.e., alarm calling) and secondarily to increased food delivery. In all treatments, post-fledging mortality was the greatest during the first week out of the nest, as has been found at north and south temperate latitudes (Green and Cockburn 2001, Naef-Daenzer et al. 2001, Sullivan 1989). We could not, however, determine the relative importance of vulnerability to predators or risk of starvation to juvenile mortality during this time period.

Our experimental manipulation of clutch size produced a novel brood size (three juveniles) that is not observed naturally in our focal species. One potential criticism of this manipulation is that the behavioral responses of adults to a brood of three juveniles may never have been subject to selection. The experimental creation of novel phenotypes, however, is an important mechanism used to investigate how natural selection may influence the distribution of a naturally occurring trait (Ketterson and Nolan 1992, Ketterson et al. 1996). In this study, the inclusion of a three-egg clutch treatment helps distinguish at what stage during the nest cycle selection may be acting most strongly to limit clutch size. The birds did respond to the enlarged brood

treatment by increasing their feeding rate to nestlings and by single adults assuming sole care of two juveniles on the day of fledging. Even if enlarged broods are excluded from these analyses, a comparison of reduced and control broods reveals the same patterns; namely, a lack of support for the nest predation and food limitation hypotheses and a strong effect of brood size on post-fledging juvenile survival.

The inverse relationship between brood size and post-fledging survival suggests that the small clutch of tropical birds maximizes fecundity during the post-fledging period rather than during the nestling period. We also found that the greater number of fledged juveniles produced by larger broods offsets the reduction in their post-fledging survival. Consequently, the number of dispersing juveniles per single nest attempt, and, by extension, the number of potential recruits to the breeding population, was similar for all clutch sizes. This result does not support the critical component of Lack's (1947) hypothesis that individuals lay the number of eggs that maximizes the reproductive output of that clutch.

Overall, only 19.8% of nests in this study population ($n = 328$) produce fledged juveniles (Styrsky 2003). Because of high rates of nest predation, pairs of Spotted Antbirds attempt, on average, five clutches per year, but less than one clutch per pair is successful (Styrsky 2003). In this environment, the distribution of reproductive effort among multiple breeding attempts may have a greater impact on fecundity than an increase in reproductive effort for a single breeding attempt (Murphy 1968, Hirshfield and Tinkle 1975). Laying an additional egg would not increase the productivity of the few successful clutches because of the negative effect of brood size on post-fledging juvenile survival. Furthermore, an extra egg could be more energetically expensive to the adults, both in terms of additional resources needed for egg production and an increase in nestling feeding rate to larger broods. Experiments with tropical birds that test the effect of repeatedly raising larger broods on adult survival and future fecundity are needed to evaluate this hypothesis. Single-egg clutches may not be advantageous, however, as a second egg in the clutch could provide insurance against hatching failure (8.4% in this study population, $n = 249$ eggs) and increase the probability that at least one juvenile per clutch escapes predation during the post-fledging period. Consequently, the production of a two-egg clutch could represent a bet-hedging strategy whereby fecundity is maximized by spatially and temporally distributing the production of offspring among multiple breeding attempts.

This study is one of few to experimentally test hypotheses of clutch size evolution for a tropical bird species and the only one to focus on an open-cup-nesting, forest-interior bird. Our results do not support two classic hypotheses for clutch size evolution in tropical habitats. Instead, this experiment reveals that post-

fledging mortality is an important selection pressure influencing the fecundity of Spotted Antbirds. More experimental studies of a wider range of tropical and south temperate species are needed to clarify the role of extended post-fledging parental care and potential life-history trade-offs on the clutch size of birds in these regions.

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LITERATURE CITED

- Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* **82**:2948–2960.
- Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: How do species traits vary from the poles to the equator? *Journal of Animal Ecology* **71**:79–87.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**:307–343.
- Green, D. J., and A. Cockburn. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* **70**:505–514.
- Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. U.S. Fish and Wildlife Service Technical Report **24**:1–7.
- Hirshfield, M. F., and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences (USA)* **72**:2227–2231.
- Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs* **41**:207–233.
- Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, and J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? *American Naturalist* **136**:277–291.
- Ketterson, E. D., and V. Nolan, Jr. 1992. Hormones and life histories: an integrative approach. *American Naturalist* **140**:S33–S62.
- Ketterson, E. D., V. Nolan, Jr., M. J. Cawthorn, P. G. Parker, and C. Ziegenfus. 1996. Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature. *Ibis* **138**:70–86.
- Lack, D. 1947. The significance of clutch size. *Ibis* **89**:302–352.
- Lack, D. 1948. The significance of clutch size. Part III. Some interspecific comparisons. *Ibis* **90**:25–45.
- Levings, S. C., and D. M. Windsor. 1982. Seasonal and annual variation in litter arthropod populations. Pages 355–387 in E. G. Leigh, Jr., A. S. Rand, and D. Windsor, editors. *The ecology of a tropical forest*. Smithsonian Institution, Washington, D.C., USA.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101–127.
- Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**:1–10.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* **287**:1482–1485.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**:456–466.
- Moreau, R. E. 1944. Clutch size: a comparative study, with reference to African birds. *Ibis* **86**:286–347.
- Murphy, G. I. 1968. Pattern in life history and the environment. *American Naturalist* **102**:391–403.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**:730–738.
- Ricklefs, R. E. 1969. The nesting cycle of songbirds in tropical and temperate regions. *Living Bird* **8**:165–175.
- Robinson, W. D., T. R. Robinson, S. K. Robinson, and J. D. Brawn. 2000. Nesting success of understory forest birds in central Panama. *Journal of Avian Biology* **31**:151–164.
- Russell, E. M. 2000. Avian life histories: Is extended parental care the southern secret? *Emu* **100**:377–399.
- SAS Institute. 1999. SAS OnlineDoc. Version 8. SAS Institute, Cary, North Carolina, USA.
- Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* **91**:430–455.
- Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Pages 575–594 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. *Neotropical ornithology*. Volume 36. American Ornithologists' Union, Washington, D.C., USA.
- Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* **54**:159–169.
- Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *Journal of Animal Ecology* **53**:945–953.
- Styrsky, J. N. 2003. Life-history evolution and population dynamics of a Neotropical forest bird (*Hylophylax naevioides*). Dissertation. University of Illinois, Urbana, Illinois, USA.
- Styrsky, J. N. 2005. Influence of predation on nest-site reuse by an open-cup nesting Neotropical passerine. *Condor* **107**:133–137.
- Sullivan, K. A. 1989. Predation and starvation: age specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology* **58**:275–286.
- Systat. 2004. Systat. Version 11. Systat Software, Richmond, California, USA.
- Willis, E. O. 1972. The behavior of Spotted Antbirds. American Ornithologists' Union, Washington, D.C., USA.
- Yom-Tov, Y., M. I. Christie, and G. J. Iglesias. 1994. Clutch size in passerines of southern South America. *Condor* **96**:170–177.