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TRY AND TRY AGAIN: NEST PREDATION FAVORS PERSISTENCE IN A NEOTROPICAL BIRD

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Resumen. – Intentar y intentar de nuevo: la depredación en los nidos favorece la persistencia en una ave Neotropical. – El éxito reproductivo de las aves que viven en sistemas con altas tasas de depredación puede ser explicado por medio de dos hipótesis. La primera se refiere a que la depredación de los nidos se evita, ya sea por la ubicación del nido, por selección del territorio, por el comportamiento de los padres, o por otros. Esta hipótesis predice que las parejas pueden mostrar una consistencia en el éxito reproductivo debida a la evasión de la depredación. Una hipótesis alternativa es que las parejas varían en su habilidad para volver a anidar después de un intento fracasado de anidación. Dicha hipótesis predice que la diferencia en el éxito reproductivo de cada pareja se debe a esta habilidad y no al hecho de que se esté evitando la depredación en el nido. Para probar estas hipótesis, estudiamos el éxito reproductivo, los intervalos de anidación, la duración del periodo reproductivo y la historia de anidación del Batará Plomizo (*Thamnophilus atrinucha*) en la región central de Panamá. Encontramos que el éxito reproductivo es bajo, con una tasa de sobreviviencia de nido de 0.91 dia^{-1}; sólo uno de cada ocho intentos de anidación es exitoso y esencialmente todos los fracasos se deben a la depredación del nido. Las parejas no mostraron consistencia en el éxito del nido ni variación en su habilidad para evitar la depredación. Al contrario, la habilidad de anidar de nuevo varió entre parejas y, tras el fracaso de anidación, las parejas con experiencia volvieron a anidar 14 días antes que las parejas sin experiencia. En promedio, los intervalos más breves entre anidaciones permitían tres intentos más por año. Ya que sólo uno de cada ocho nidos tiene éxito, y que en promedio la pareja anida cinco veces por año, las oportunidades adicionales de anidación proveen el margen necesario para aumentar las probabilidades de éxito reproductivo. Mientras que las estrategias de anidación pueden explicarse por la evasión de la depredación, todos los intentos de anidación son igualmente susceptibles de fracasar. Por el contrario, la habilidad para volver a anidar es un factor importante que influye sobre la diferencia del éxito de anidación, y probablemente es más importante para las aves tropicales, en las cuales las largas temporadas reproductivas permiten varios intentos de anidación.

Abstract. – Successful reproduction for birds in systems with high nest predation rates may be explained by two alternatives. The first hypothesis is that nest-predation is avoided, perhaps by nest-site or territory selection, parental behavior and so on. This hypothesis renders the prediction that within-pair consistency, or repeatability, in nesting success occurs and is due to nest predation avoidance. The alternative hypothesis is that pairs vary in their ability to nest again following predation, and generates the prediction that differential reproductive success among pairs is due to renesting ability, not predation avoidance. To test these alternatives, nest success, renesting intervals, breeding season length, and nesting history were studied in the Western Slaty Antshrike (*Thamnophilus atrinucha*) in central Panamá. Reproductive success is low; with a survival rate of 0.91 day^{-1}, only one in eight nesting attempts are successful and essentially all nest failures are due to nest predation. Pairs showed neither consistency in nesting success nor variation in nest

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predation avoidance. Renesting ability, however, varied among pairs and, following nest failure, experienced pairs renested 14 days sooner than inexperienced ones. On average, reduced renesting interval allowed time for an additional three nesting attempts year^{-1}. Since only one in eight nests is successful and the average pair nests five times year^{-1}, these additional nesting opportunities provide the margin necessary to increase the odds of successful reproduction to near certainty. While nest predation avoidance may explain nesting strategies, all nesting attempts are equally likely to fail. Instead, renesting ability is an important factor influencing differential nesting success, and is probably more important for tropical birds, where long breeding seasons permit several nesting attempts. *Accepted 21 April 2005.*

Key words: Reproductive success, nest predation, persistence, renesting interval, Western Slaty Antshrike, *Thamnophilus atrinucha.*

INTRODUCTION

Nest predation is one of the most important causes of nest failure in passerine birds (Nice 1957, Ricklefs 1969) and hence may have been an important factor in the evolution of avian life histories (Lack 1947, 1948a, 1948b, 1949, 1954; Skutch 1949, 1966, 1985; Ricklefs 2000). Differential nest predation across latitudes may also have influenced latitudinal variation in avian life-histories, since nest predation rates are often higher for tropical birds (Skutch 1985, Kulesza 1990, Martin 1996, Sæther 1996). Therefore, nest predation may have far-reaching influences on many aspects of reproduction in birds.

Nest-site selection may reduce nest predation risk at nests by making nests more difficult for predators to find (Martin & Roper 1988). If nest-site selection is repeatable and heritable, then natural selection can act to favor some birds because their preferred nest sites yield greater nesting success. For example, Pinyon Jays (*Gymnorhinus cyanocephalus*) alter nest site selection based on the cause of previous nest failure (Marzluff 1988). While nest predation has been shown to be associated with nest-sites (Blancher & Robertson 1985, Murphy 1983, Rands 1988, Martin & Roper 1988, Holway 1991, With 1994), no studies have shown nest-site selection to be either repeatable or heritable. Showing heritability requires that tendencies for selection of nest-sites by individuals be estimable or measurable, and second, that offspring show similar tendencies as their parents (Endler 1986). However, in nature, small passerines may not nest often enough in their lifetimes to provide a sample size of nesting attempts that is large enough to allow a reliable estimate of nest-site selection tendencies, or of consistency in nesting-success.

Demonstrating consistency in nesting success is a prerequisite for demonstrating that birds may avoid predation. That is, a nest may be successful by chance or by choice of nest site. Chance is mere luck, while choice implies that birds recognize quality in nest sites. For natural selection to favor nest-site choice, then birds must be consistent in that choice. At least three possibilities may be important in consistency of nest predation avoidance: 1) Pairs show high repeatability in their choice of nest sites and these sites are repeatable in avoiding nest predation; 2) behavior may be associated with nest success in that displays to distract predators may vary among adults and that variation is associated with nest success; 3) predator density could be variable on a scale that makes some territories relatively predator-free, and so these territories may have greater reproductive success. All of these possibilities share the same null hypothesis (all pairs show equal tendencies, or consistency, with respect to nest predation). Therefore, testing for that consistency is the first step in testing which of these, or other, possibilities are important for avoiding predation. Conversely, inconsistent breeding performance would suggest that nest predation is random among nesting attempts and no pairs of birds avoid predation any better than other pairs, and the alternative hypotheses need not be tested.

Unfortunately, demonstrating consistency in breeding performance is difficult or impossible in short-lived birds because they may have few lifetime nesting attempts and the chance that all of these attempts will be recorded is small. Testing consistency in breeding performance requires relatively long-lived species and many nesting attempts to provide the sample size necessary to compare pairs. Such species can also provide the sample size necessary for testing alternative hypotheses to explain how birds breed successfully despite high nest predation rates. For example, one alternative suggests that individuals may vary in their ability to renest and in the number of nests they may attempt in any given year (Slagsvold 1984, Filliater *et al.* 1994).

Here I describe tests of the hypothesis of consistency in nest-success and the alternative hypothesis of renesting ability to explain how birds cope with high nest-predation rates. Specifically, I tested 1) whether pairs showed inherent and consistent trends in nesting success (by avoiding nest predation), and 2) whether learning influenced nest predation avoidance in which experienced birds were predicted to be better than naive birds at avoiding nest predation. The alternative hypothesis tested was whether renesting rates varied among experienced and naive birds and could explain how birds breed successfully in any given year despite high predation rates.

METHODS

Study site. This research took place in forests of central Panamá, in the Parque Nacional Soberanía, approximately 8 km northwest of the town of Gamboa (see Roper 1992, 2000, 2003; Sieving 1992, Roper & Goldstein 1997). This study was carried out from mid May to late August of 1990, 1991, and 1992, and for the entire year of 1993.

Study species. The Western Slaty Antshrike (*Thamnophilus atrinucha*) is a common understory bird in forests from Mexico to southern South America (Ridgely 1976, Hilty & Brown 1986, Ridgely & Tudor 1989, Stiles & Skutch 1989, Isler *et al.* 1997). Western Slaty Antshrikes are monogamous, territorial and easily observed. Nests are built in the forks of slender, horizontal branches of trees or shrubs with an average height of 2.3 m. A clutch size of two eggs is invariable. Both adults share all phases of rearing young: nest-construction, incubation, feeding nestlings and so on. Males feed females prior to egg laying at the end of nest construction and just before egg-laying (also see Oniki 1975). Birds were captured with mist-nets and uniquely color-banded and released at the site of capture. Color-banded birds were then observed to find their nests, record their breeding sequence and nesting success.

Nests and nesting success. Nests were found by searching the appropriate strata of the forest understory, and by following birds during nest construction or feeding young in nests, when they conspicuously carry nest material or food to their nests or young. To check nests, when necessary, a mirror was held over the nest to inspect the nest contents. When necessary, the mirror was placed at the end of a pole to reach higher nests. Otherwise, nest contents were visible from a distance. Nests were checked every two to three days, at the greatest distance possible, often as far as 30 m from the nest, to minimize potential but unlikely observer effects at nests (Götmark 1992). Nests were closely approached only to check their status when found, to examine when eggs were laid, when they hatched, and to band fledglings. From these data, nest predation rates, renesting intervals and breeding season length, and nesting consistency were estimated. Breeding season length was estimated as the interval from the beginning of the first nest to the last date of activity of the last nest. Also, breeding season length was calculated following Ricklefs & Bloom (1977). This calculation considers that breeding is not equally intense in all months, and is calculated as follows:

$$B = 30 \text{ x } e^{-\Sigma p_i \log_e p_i}$$

where B = breeding season length in days, and p_i = the proportion of nests initiated in month i, and multiplying by 30 estimates the number of days, rather than months, of breeding.

Consistency in reproductive success. While consistency in breeding performance may result from several causes (good nest-sites, low predation in some territories, and so on), all of the causes share a common null hypothesis. That is, a heritable component to nest predation avoidance requires consistency in breeding performance within pairs. Thus, the null hypothesis (H_{null}) is: all pairs of birds have the same probability of nest predation, with the alternative ($H_{alternative}$): some pairs of birds are more effective at avoiding predation than other pairs.

The alternative does not specify how birds may avoid predation. Indeed, if and only if the null hypothesis is rejected is it necessary to specify how pairs might avoid predation to test those specific predictions. Therefore, nest consistency must first be tested and rejected if possible. Two types of tests for consistency in predation avoidance were used. This allowed the best use of the data since not all nests provide complete nesting information and to reduce the possibility of not rejecting a false null hypothesis (Type II error). First, the number of days unsuccessful nests survived was compared among pairs. Unsuccessful attempts must be used for the following reasons: 1) the number of days all nests survived is not a continuous variable (it is called censored), because all successful nests have equal nesting period lengths. These censored data do not conform to the assumptions of ANOVA, 2) comparing survival of unsuccessful nests does conform to the assumptions of ANOVA (normal residuals, equal variances); and 3) if pairs vary in their ability to avoid predation, the average number of days failed nests survive should vary among pairs where high-quality pairs avoid predation longer than low-quality pairs. Thus, to test for within-pair consistency in predation avoidance, the average duration of unsuccessful nesting attempts was compared among pairs with five or more nesting attempts in 1993 (ANOVA, α = 0.05). Similarly, to test whether experience (learning) is important in predation avoidance, birds were grouped into three experience classes based on the number of years nesting on the study area (one, two and three or more). In this analysis, the average number of days nests survived was calculated for each pair, and that average was then used in the ANOVA to test the prediction that some pairs avoid predation better than others.

Next, survival analysis (Cox regression, JMP version 4.05, 2002) was used to include all nests (successful and unsuccessful) in the comparisons. In this analysis, pairs were not compared because of small sample sizes per pair. Instead, only experience was analyzed and pairs were grouped in the following experience classes: one attempt versus more than one; breeding in only one year versus breeding in more than one; in 1993, first time breeders in 1993 versus return breeders. In these analyses some pairs contribute more than others to the total sample size, especially those pairs that remained on the study area the longest. If these pairs were consistent (repeatable), then we should show that expe-

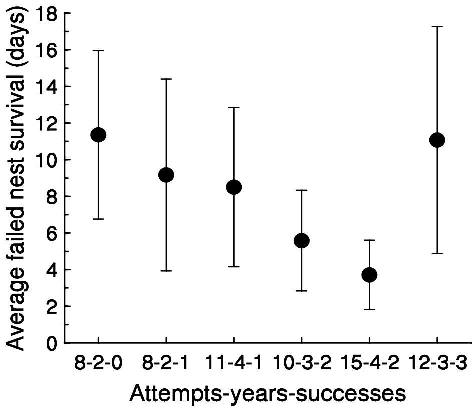

FIG. 1. Average failed nest survival in days (± 95% confidence interval) of six pairs with five or more attempts in 1993. The X-axis is labeled with the total number of nesting attempts – total number of years observed nesting – total number of successes in order of number of successes. All pairs have similar nest survival (ANOVA, NS, sample size for each pair may be calculated by subtracting successes from the total.).

rience is important by rejecting the null hypothesis. Alternatively, if pairs are not repeatable, then, irrespective of pair, each nesting attempt is an independent random event that fails to support the alternative hypothesis of consistent performance.

Persistence and reproductive success. One alternative hypothesis to consistency in nest predation avoidance is that renesting intervals are consistent (repeatable) within pairs. If so, then consistent and rapid renesting following nest predation should increase the probability of nest success within any breeding season. Renesting after success requires an extended period of post-fledging care and so does not enter into this calculation. The complete nesting history of pairs in 1993 allowed calculation of post-predation renesting intervals. Thus, to test the prediction that experience is important for renesting ability, renesting intervals were compared among pairs in two experience levels: birds that nested two years or less (naive) and birds that nested more than two years (experienced) using Student's t-test. These experience classes were chosen because they present similar sample sizes, equal variances and normal distributions. Experience classes should estimate well the true experience levels since these birds are permanently monogmous and territorial.

RESULTS

Nest predation and nesting successs. Thirty of 212 (14%) nest attempts were successful. Nest predation caused the failure of 149 of the remaining 182 nests (70% of all nests, 82% of all failures). Twenty-nine nests were initiated but were never observed with eggs, and thus failed for unknown reasons. Of the remaining 153 failed nests, nest predation caused the failure of 149 (97%), and so clearly nest predation is the most important cause of nest failure. Mayfield method (Mayfield 1961, 1975; Hensler & Nichols 1981) estimates of nest survival over all years was 0.91 day^{-1} (SD = 0.007, based on a sample of 186 nests). Nest predation did not vary among years, and so years were pooled when possible for the subsequent tests.

The nesting cycle. The interval from the beginning of nest construction to egg laying varied from one to 90 days (mean ± SE = 6.4 ± 1.5, N = 70). Three intervals were very large (greater than 14 days), and when these three outliers were removed, the interval was from one to 13 days (4.2 ± 0.5, N = 67). The average nesting attempt in 1993 lasted 10.3 days (SE = 0.7, N = 105, median = 8.5 days). The average unsuccessful nesting attempt in 1993 lasted 8.3 days (SE = 0.67, N = 87, median = 6.5 days). Renesting intervals after nest failure were calculated in 1993 (all nesting attempts for some pairs were known) and varied

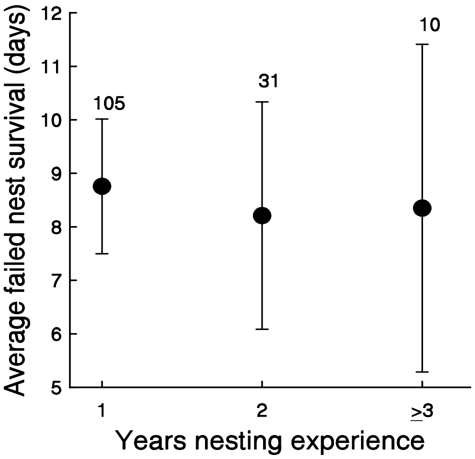

FIG. 2. Average failed nest survival in days (± 95% confidence interval) grouped by number of years observed nesting on the study site. Average nest survival is similar among all levels of experience (ANOVA, NS).

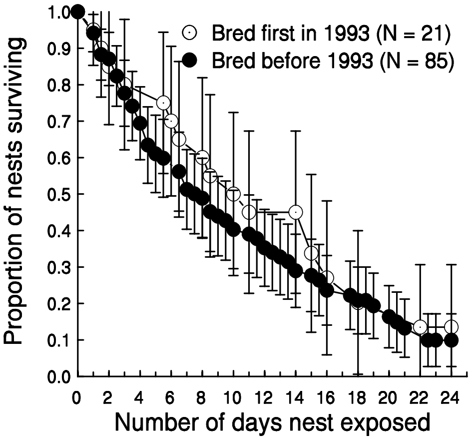

FIG. 3. Survival analysis of nesting success in 1993 comparing pairs that nested prior to 1993 with those that nested for the first time in 1993 (proportional hazards regression). Experienced pairs and inexperienced pairs have similar survival curves ($P > 0.05$).

between five and 72 days (19.1 ± 1.6, N = 66). In 1993, the breeding season length was 225 days (following Ricklefs & Bloom 1977), and the first nests were started prior to 1 January (already in progress when found on that date) and the last nest failed around 1 October (an absolute interval of about 273 days).

Consistency in reproductive success. All pairs of birds had fewer successful than unsuccessful nesting attempts, including two pairs that each had two successes in 1993. Six pairs of birds in 1993 (when the entire breeding season was studied) attempted five or more nestings (permitting ANOVA), and the average nest duration (number of days survived) of unsuc-cessful nests was the same among these pairs (ANOVA, $P > 0.10$, Fig. 1). The pair with the most nesting attempts in the course of the study (N = 15) had the lowest average nest survival. One pair with three successes (in 12 attempts) had the same average survival as a pair with no successes (in 8 attempts). Thus, the first step (pairwise differences in nest predation) in testing the hypothesis that pairs of birds are consistent in nest predation avoidance was not supported.

Experienced birds showed no greater tendency to avoid nest predation than naive birds (Fig. 2). The average survival of unsuccessful nests was essentially identical regardless of number of years of experience nesting (ANOVA, $P > 0.05$). When all nesting attempts, including successes, were compared, experience still showed no consistency in avoiding predation. This result held regardless of how experience was calculated (Fig. 3) and so the hypothesis that experience influences nest survival rates was also not supported. Antshrikes apparently do not learn to reduce predation risk after nest predation.

Persistence and reproductive success. Western Slaty Antshrikes are considered permanently monogamous, and most pairs were monogamous during the study (86%). Nine males and

TABLE 1. Average renesting intervals (in days) and the average number of nesting attempts possible year^{-1} with two breeding season length estimates, with 95% confidence intervals (C.I.), compared by experience and sex. The average number of nesting attempts per year was calculated by dividing the breeding season length [first value following Ricklefs & Bloom (1977) – 225 days; second value using the absolute interval from first to last nest – 273 days] by the fixed nesting interval (construction and egg-laying of 4.2 days and the average nest duration of 8.3 days) plus the renesting interval and its 95% confidence interval.

Sex	Experience (years)	Renesting interval ± 95% C.I.	Nesting attempts year^{-1}	Lower C.I.	Upper C.I.
Female	> 3	17 ± 3	7–9	6–8	8–10
	< 3	30 ± 6	5–6	4–5	6–7
Male	> 3	19 ± 7	7–8	5–7	8–10
	< 3	27 ± 6	5–6	4–6	6–8

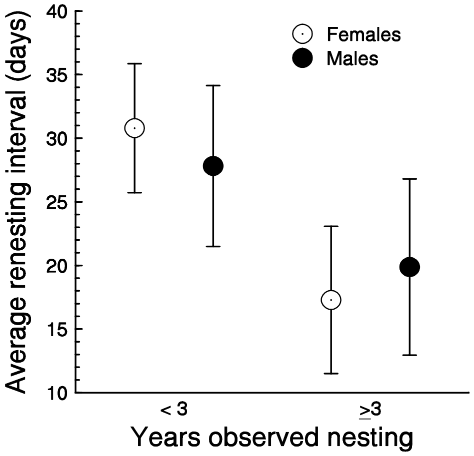

FIG. 4. Average renesting intervals (± 95% CI) for females and males by experience (years nesting on study area, < 2 year, ≥ 2 year). Experienced birds renest more quickly following nest failure (t = 4.5, df = 21 for females, and t = 2.2, df = 20 for males, both *P* < 0.05).

seven females (or nine pairs) in 63 total pairs of birds (14%) lost or changed mates. To best use the data, sexes were separated for the comparison of experience and renesting intervals. Student's *t*-tests were based on log-transformed renesting intervals after predation. Both sexes with experience renested more quickly than naive birds (Fig. 4). After failure, experienced females renest on average approximately 14 days sooner than naive females (17 versus 31 days, $t_{21} = 4.5$, $P < 0.05$). Experienced males renested 8 days sooner than naive males (20 days versus 28 days, $t_{20} = 2.2$, $P < 0.05$, Table 1), and so the hypothesis that experience influences renesting interval was supported.

DISCUSSION

Many avian life-history studies have concentrated on nest predation and how birds might avoid nest predation without considering other aspects of the birds' life histories that may be important (Martin 2004). For example, nest predation experiments have been widely used to examine nest predation, even when those experiments have been shown to be problematic (Roper 1992, 2000, 2003). Yet, other aspects of birds' reproductive tactics have received little attention. Here I show that variable renesting intervals, rather than predation avoidance, are important in a system with very high nest predation rates.

Nest predation was the only important cause of nest failure, yet Western Slaty Antshrike pairs showed no consistency in avoiding predation. Many studies have shown that nest-sites may influence nesting success (Sieving 1992, Martin & Roper 1988, Martin 1995, Cresswell 1997, Sieving & Willson 1998, but see Schmidt & Whelan 1999, Roper 2003), but none of these studies attempted to show that individual pairs were consistent in their site selection and in their ability to avoid predation. Nesting performance in nature is difficult to measure and it is even more difficult to obtain adequate sample sizes. Yet, without showing consistency in breeding performance, the suggestion that natural selection influences nest-site selection is problematic.

Here, nesting pairs showed no trend in either innate or learned ability to avoid predation. Nest predation probability is random among pairs of Western Slaty Antshrikes and average survival of failed nests was not associated with number of successful nests. One of the pairs with the lowest average survival rates had the greatest number of nest successes (Fig. 1). Average daily survival of failed nests was also random with respect to experience (Figs 2 and 3), showing that pairs do not learn to avoid predation. A natural-experimental study of nest-sites at this same location showed that while sites may influence predation, the influence is very weak and may be contradictory where two negatively correlated variables may be positively correlated with nest-site quality (Roper 2003). Thus, one variable may negate the benefit of another variable. Perhaps those components of nest-sites that may influence predation are too vague for birds to be able to select sites with those components. Clearly, on some scale, nest-sites are hidden to avoid predation, but perhaps the tendency for nest-site selection is a species-wide character and all individuals use the same criteria when selecting a nest site. If so, then the variation among sites may be due more to variation in vegetation in the area than it is to actual nest-site selection.

Renesting ability, however, is associated with experience and may provide fitness benefits. Following nest predation, experienced birds renest more quickly than naive birds (Fig. 4). How large is the benefit from reduction of the renesting-interval in terms of annual reproduction? With a 225 or 273 day breeding season, a 4.2 day average interval from initiation of nest construction to egg laying, an 8.3 day average duration of failed nest attempts and renesting intervals for naive versus experienced birds, experienced females may have 8–9 breeding attempts per year compared to 6–7 for naive females (males 6–10 and 5–8 respectively). Given that the probability of nest success did not differ between experienced and inexperienced birds (1 success in 8 attempts), only experienced birds would have the eight or more attempts required per year to insure successful nesting. Success of experienced breeders may therefore come from their ability to reduce renesting interval and squeeze more attempts in per season.

This pattern, the ability to renest quickly, may greatly influence reproductive success in a variety of species. Juncos (*Junco hyemalis*) apparently minimize post-fledging parental care to provide time to renest, thereby increasing annual reproductive success (Sullivan 1988). Northern Cardinals (*Cardinalis cardinalis*) seemed unable to avoid predation and renesting ability was suggested as a possible alternative (Filliater *et al.* 1994). Perhaps the patterns that Skutch (1949) attributed to nest predation avoidance were in fact patterns associated with renesting ability. That is, high nest predation rates favored smaller clutches because with less energy spent per clutch, more clutches are possible in any given year (Slagsvold 1984) and the renesting interval may be reduced with smaller clutches. This pattern may also explain the latitudinal trend in parental care in which tropical birds do not defend nests (compared to temperate birds) because the odds of their own survival without nest defense are better than the odds with nest defense (Ghalambor & Martin 2001). Hence, nest predation may have selected for reduced clutch size as Skutch suggested, but for different reasons. Persistence, rather than nest predation avoidance, could be an important part of the evolutionary process that resulted in differences between temperate and tropical passerine life histories.

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