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ARE ARTIFICIAL BIRD NESTS EFFECTIVE SURROGATES FOR ESTIMATING PREDATION ON REAL BIRD NESTS? A TEST WITH TROPICAL BIRDS

W. DOUGLAS ROBINSON,^{1,3} JENNIFER NESBITT STYRSKY,^{2,4} AND JEFFREY D. BRAWN²

¹*Oak Creek Laboratory of Biology, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, Oregon 97331, USA; and*

²*Department of Animal Biology, 606 East Healey Street, University of Illinois, Champaign, Illinois 61820, USA*

ABSTRACT.—Artificial bird nests are often used in studying birds whose nests are difficult to find, such as those of many tropical species. Yet the underlying assumption that predation on artificial nests accurately estimates predation on real nests may be invalid. We compared rates at which contents of real and artificial nests were lost to predators in a Panamanian rainforest. We attempted to make artificial nests as realistic as possible by moving real, undamaged nests to species-typical nest sites in a study area where the same species were actively breeding. Characteristics of new sites for the moved nests were statistically similar to nest sites chosen by birds. We baited nests with two quail eggs and monitored them for species-specific incubation periods. Predation on real and artificial nests was dissimilar in three of four species, revealing that predation on artificial nests correlated poorly with predation on real nests. In a fourth species, artificial and real nests were lost at similar rates. The latter result may have occurred by chance, because depredated real nests rarely showed any sign of damage; whereas depredated artificial nests were torn, which suggests that real and artificial nests attracted different predators. Our results indicate that artificial nests, even when built by the species themselves and placed in realistic situations, are poor predictors of real nest success and we caution against their use in the tropics. *Received 9 October 2003, accepted 3 January 2005.*

Key words: artificial bird nests, daily predation rate, nest predation, Panama, tropical forest.

¿Son los Nidos Artificiales Sustitutos Efectivos para Estimar la Depredación de Nidos Verdaderos? Una Prueba con Aves Tropicales

RESUMEN.—Frecuentemente se utilizan nidos artificiales para estudiar especies de aves cuyos nidos son difíciles de encontrar, como es el caso de muchas especies tropicales. Sin embargo, la suposición subyacente de que la depredación de nidos artificiales predice con exactitud la depredación de nidos naturales puede ser inválida. Comparamos las tasas de pérdida por depredación del contenido de nidos artificiales y reales en un bosque lluvioso en Panamá. Intentamos hacer los nidos artificiales de la forma más realista posible, trasladando nidos reales y no dañados a sitios de nidificación típicos de las especies estudiadas en un área de estudio donde las especies se estaban reproduciendo. Las características de los nuevos sitios donde los nidos fueron trasladados fueron estadísticamente similares a las características de los sitios de nidificación escogidos por las aves. Colocamos

³E-mail: douglas.robinson@oregonstate.edu

⁴Present address: Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, Alabama 36849, USA.

dos huevos de codorniz en los nidos artificiales y los monitoreamos durante los períodos de incubación de cada especie. La depredación sobre los nidos reales y artificiales fue desigual en tres de las cuatro especies estudiadas, revelando que la depredación de nidos artificiales se correlaciona pobremente con la depredación de nidos reales. En la cuarta especie, los nidos reales y artificiales fueron depredados a tasas similares. Este último resultado puede haber ocurrido por azar, debido a que los nidos naturales depredados raramente presentaron signos de destrucción, mientras que los nidos artificiales fueron destrozados, lo que sugiere que los nidos reales y artificiales atrajeron depredadores diferentes. Nuestros resultados indican que los nidos artificiales, incluso cuando son construidos por las mismas especies y puestos en situaciones realistas, predicen pobremente el éxito de los nidos naturales y recomendamos precaución sobre el uso de nidos artificiales en los trópicos.

MEASUREMENTS OF REPRODUCTIVE SUCCESS are critical for understanding the evolution of life histories (Lack 1948, 1968; Ricklefs 1969; Martin 1995), population viability (Beissinger and McCullough 2002), effects of habitat modification on populations, and, by extension, management approaches for conserving populations (Wilcove 1985). Yet direct measures of reproductive success are difficult to acquire for most kinds of organisms because of the large effort required to locate and track offspring and their survival. Studies involving birds have been particularly common, because reproductive success can be gauged by the rate at which their nests fail or fledge young (Newton 1989). Nevertheless, to accumulate sufficient data, incredible effort is often required. In the tropics, for example, studies of avian reproductive success are rare, because most species have low population densities (Karr 1971, Terborgh et al. 1990, Robinson et al. 2000a) and build cryptic nests that are visually obscured by dense tropical vegetation (Skutch 1949, 1985; Koepcke 1972). Even in temperate areas where most bird species are relatively more common and their nests are easier to locate, many investigators of avian nesting success have resorted to other methods for estimating reproductive success.

The most common of those methods is the use of artificially constructed nests baited with game-bird eggs as surrogates for real nests (Major and Kendal 1996). Artificial nests are positioned in the field and monitored to evaluate the level of predation in a given geographic location. The primary advantages of using artificial nests are (1) that nests can be quickly and easily distributed in particular arrangements so that specific hypotheses can be evaluated efficiently and (2) that artificial nests can be

monitored in large quantities, thus increasing statistical power available during hypothesis testing.

A growing body of evidence, however, suggests that use of artificial nests has serious disadvantages (Major and Kendal 1996, Thompson and Burhans 2004). One implicit assumption of most artificial nest experiments is that the method provides a proportional index of predation on real nests. That is, although real and artificial nests do not necessarily attract predators at the same rates, the relative differences are assumed to be similar enough that the results of either method lead to the same conclusions about ecological hypotheses. That assumption has been tested with increasing frequency (Moore and Robinson 2004). In most cases, predation on artificial and real nests has differed (Storaas 1988, Wilson et al. 1998, Davison and Bollinger 2000, Zarette 2002).

Nevertheless, the method continues to have appeal for those who wish to study nest predation in rare species or in communities where nests are difficult to find, such as many tropical forest bird communities (Sieving 1992, Roper 2003). Before using artificial nests in any situation, however, the degree to which predation on artificial nests mirrors predation on real nests must be quantified (Moore and Robinson 2004). To improve comparability between artificial and real nest predation rates, Major and Kendal (1996) recommended that investigators design artificial nests to maximize their similarity with real nests of the species being studied. By reducing differences in nest design, nest placement, egg characteristics, number of days eggs are exposed to predation, and other experimental protocols, investigators using artificial nests might better gauge levels of real nest predation.

Of the growing number of studies attempting to compare predation rates on artificial and real nests, all fall short of Major and Kendal's (1996) recommendations in several ways. One key shortcoming is that most studies fail to show statistically that artificial nests have been positioned in sites that are similar to sites that real birds select (Götmark et al. 1990, Reitsma 1992, Wilson et al. 1998, King et al. 1999). If site characteristics influence predation rates, as has been shown for real nests (Martin 1993, 1995), then such differences can explain the common mismatch between predation on artificial and real nests. Ideally, studies evaluating accuracy of artificial nests should simultaneously monitor predation on real nests found in the same study area and should demonstrate that artificial nests have been placed in situations that real birds would have chosen (Major and Kendal 1996).

To evaluate the accuracy of artificial nest results in a tropical setting, we studied predation on real and artificial nests concurrently in a tropical forest in Panama. We attempted to maximize the chances that artificial nests would accurately gauge real nest predation by using nests built by birds instead of manmade nests, placing the nests in sites statistically similar to sites chosen by real birds, exposing eggs to potential predation over intervals equal to species-specific incubation periods, and monitoring real and artificial nests in the same manner.

METHODS

Study area.—We conducted the study within a 100-ha area (the "Limbo plot") of tall forest in Soberania National Park, Republic of Panama. The plot is ≥ 3 km from any nonforest edge; thus, we categorize it as a forest-interior site (Robinson et al. 2000a). Most songbirds breed during the rainy season, which begins in late

April or early May, following a four-month dry season. Peak nesting activity is in the first three months of the rainy season (Robinson et al. 2000b). Additional details of the vegetation and climate of the plot are described in Robinson et al. (2000a).

Study species.—We studied real nests on Limbo plot from April through July each year from 1997 to 1999 and artificial nests in 1998. We chose four species to study: Checker-throated Antwren (*Myrmotherula fulviventris*), Spotted Antbird (*Hylophylax naevioides*), Streak-chested Antpitta (*Hylopezus perspicillatus*), and Bicolored Antbird (*Gymnopithys leucaspis*). All four species were present at Limbo in sufficient numbers to allow comparisons between real and artificial nests (Table 1). The Checker-throated Antwren constructs a pendant nest placed at the end of a thin branch; the nest often hangs 1–3 m above ground, within an open space in a vine tangle. Spotted Antbird nests are open cups typically supported by forked branches of a small sapling; most nests are 0.5–1.5 m above ground. Streak-chested Antpittas build shallow platform nests; most are placed 1–2 m above ground on a horizontal branch or palm frond. Bicolored Antbirds placed nests 0.2–2 m up in small enclosed cavities of rotting stumps or dead hanging palm fronds where the base of the frond has curled and dried so that it forms an enclosure. All species laid two-egg clutches and incubated eggs for 14–18 days (Table 1).

Artificial nests.—Our "artificial" nests were real nests that we moved after the birds who built them had abandoned them because the contents had either fledged or been depredated. Once nests were abandoned, we first measured characteristics of the site in which they were placed (see below) and then carefully removed them and transported them to a new site. We moved only nests that were clean and

TABLE 1. Comparison of life-history traits and population densities for the four study species at Limbo plot, Republic of Panama.

Species	Modal clutch size ^a	Incubation period (days) ^a	Nestling period (days) ^a	Population density (individuals per 100 ha) ^b
Checker-throated Antwren	2	19.6 \pm 0.7 (8)	13.6 \pm 1.1 (5)	166
Spotted Antbird	2	17.9 \pm 1.7 (8)	11.6 \pm 0.7 (10)	56
Streak-chested Antpitta	2	22.6 \pm 2.9 (4)	11.5 \pm 1.0 (3)	42
Bicolored Antbird	2	17 (1)	12 (1)	12

^aRobinson et al. (2000a), Styrsky (2003).

^bRobinson et al. (2000b), Styrsky (2003).

undamaged and moved them within 10 days of nest abandonment. Nests were held in place with short pieces of narrow-gauge wire when necessary. We refer to those translocated nests as "artificial" nests. We baited each nest with two *Coturnix* quail eggs and monitored them for periods equal to the species-specific incubation periods. Artificial nests were monitored during the same time that birds of all four species were actively breeding on the study plot.

Although we have no evidence that our activities might have attracted predators to nests, we took precautions to reduce such possibilities (Bart and Robson 1982, Götmark 1992, Ralph et al. 1993). First, we were careful not to create obvious trails to nests and approached nests during checks from more than one direction. Furthermore, rain falls daily during the breeding season, and any scent-trails created by humans are probably ephemeral. Second, we conducted many other activities within the study area, such as mist netting and point counting, that would not lead predators to nests, reducing chances that predators following us would be rewarded. Finally, real and artificial nests were all treated in the same manner, so that any effects of observer visits should be unbiased. An exception might be if visits evoke alarm calls from adults, which in turn attract predators. Although we did not quantify such responses, we noted that all four species usually moved away from their nests when we approached and, if alarm calls were given, they were usually uttered at a distance from the nest.

We compared the nest-site characteristics of real and artificial nests to determine whether we placed artificial nests in situations similar to those chosen by real birds. We focused assessments on visual conspicuousness of nests and height above ground. At each nest, we estimated visually (to nearest 10%) the percentage of the nest visible from 2 m above ground at distances of 1, 5, and 10 m. Estimates were made at each distance from each of the four cardinal directions. We also estimated the percentage of visibility from 1 m above the nest and 0.5 m below. Nest height was measured from ground to the lowest point on the nest opening (open-cup nesters) or bottom of the entrance (cavity nesters) with a tape measure (to the nearest centimeter).

Calculations of nest success and data analyses.—We measured predation on nests by monitoring

them every three days. We calculated rates of nest predation on a per-nest basis, ignoring partial brood losses, because partial predation was rare (Robinson et al. 2000b, Robinson and Robinson 2001). We used the Mayfield (1961, 1975) method to calculate daily predation rates for both artificial and real nests. The initial day on which artificial nests were exposed to potential predation was always known. Many real nests, however, were discovered after egg laying began, so real nests particularly invulnerable to predation may have been discovered more often than those likely to be depredated soon after egg laying. That potential sampling bias was minimal (Robinson et al. 2000b). For both real and artificial nests, the exact number of days that nests were exposed was unknown, because predation was rarely witnessed. Thus, when previously active nests were found to be empty, we used the mid-point between the penultimate and ultimate inspections as the date of failure.

We used the statistical program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989) to compare predation rates of nests. The program is based on establishing variance-covariance matrices that contrast two or more nest survival rates and then comparing their differences with a chi-square distribution.

Nest-site selection analyses.—We tested for normality of distributions with a Shapiro-Wilks test. Some percentage data describing nest visibilities were not normally distributed and were arcsine-transformed before analyses. When transformation did not correct distributional problems, we used nonparametric tests. For comparisons of nest visibilities, we first averaged the visibility scores from each of the four cardinal directions for each of the three distances (1, 5, and 10 m). All analyses were conducted on those mean values. We used *t*-tests when data were distributed normally, and Wilcoxon-Mann-Whitney tests when they were not. We set $\alpha = 0.05$ and conducted all analyses with JMP software (SAS Institute 2001).

RESULTS

We discovered and monitored 418 real nests over the three years of the study. In 1998, when we conducted the artificial nest study simultaneously, we monitored 124 nests of the four target species. Most of the Spotted Antbird nests in the 100 ha were discovered as part of

an intensive study of that species (Styrsky 2003). We probably found only a small fraction of the Streak-chested Antpitta and Checker-throated Antwren nests at Limbo, because both species were common (Table 1). Few real Bicolored Antbird nests were found (five to eight each year), in part because of the lower population density of the species and the cryptic characteristics of their nests.

than artificial nests. Heights of real Checker-throated Antwren nests averaged 43 cm greater than artificial nests, and real Checker-throated Antwren nests were 10% more visible from a distance of 1 m than the species' artificial nests. Otherwise, we chose sites for artificial nests that were statistically similar to those selected by real birds.

NEST PLACEMENT

With three exceptions, placement characteristics of artificial and real nests were not statistically different (Table 2). Real nests of Bicolored Antbirds averaged 30 cm higher above ground

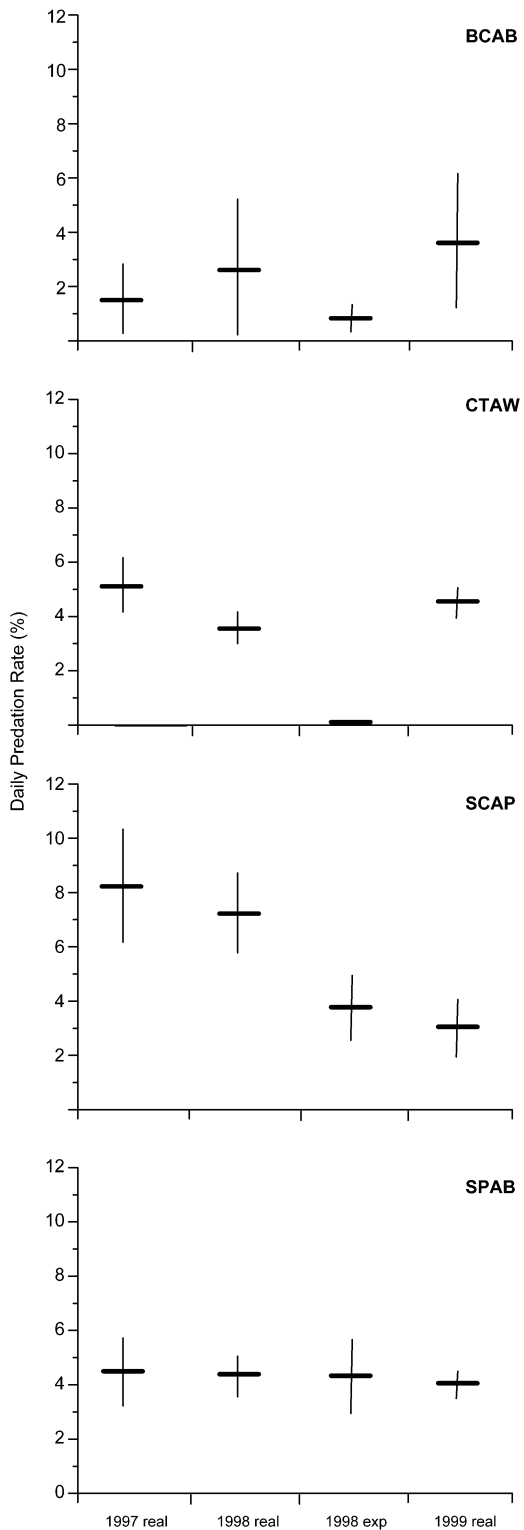
NEST PREDATION

During incubation in two of the four species, predation on artificial nests was significantly different from predation on real nests (Fig. 1). No artificial Checker-throated Antwren nests were depredated, whereas 43% of real

TABLE 2. Sites in which real and artificial nests of the four species were placed were mostly statistically similar. Means ± SE are reported. NS = not significantly different.

	Real	Artificial	
Spotted Antbird			
<i>n</i>	27	15	
Height (cm)	79 ± 34	80 ± 26	NS
Nest visibility: 1 m (%)	73 ± 2.5	79 ± 2.0	NS
5 m	60 ± 3.0	62 ± 4.9	NS
10 m	28 ± 3.6	42 ± 6.6	NS
Above	64 ± 6.4	61 ± 7.2	NS
Below	87 ± 4.0	93 ± 3.9	NS
Checker-throated Antwren			
<i>n</i>	20	11	
Height	124 ± 46	108 ± 55	NS
Nest visibility: 1 m (%)	83 ± 4.5	70 ± 5.9	<i>P</i> = 0.044
5 m	43 ± 4.4	35 ± 5.2	NS
10 m	14 ± 2.7	15 ± 4.4	NS
Above	78 ± 7.3	35 ± 6.4	<i>P</i> = 0.0002
Below	93 ± 3.2	97 ± 1.9	NS
Streak-chested Antpitta			
<i>n</i>	16	16	
Height	72 ± 30	88 ± 41	NS
Nest visibility: 1 m (%)	75 ± 4.4	82 ± 2.8	NS
5 m	44 ± 5.6	45 ± 5.7	NS
10 m	25 ± 4.7	23 ± 4.3	NS
Above	55 ± 8.1	56 ± 10	NS
Below	74 ± 8.7	58 ± 7.2	NS
Bicolored Antbird^a			
<i>n</i>	15	12	
Height	76 ± 44	36 ± 12	<i>P</i> = 0.01

^a Visibility measures of Bicolored Antbird nests are not reported, because all nests were in enclosed cavities, so that nest cups were not visible from distances of ≥1 m.



nests were lost ($\chi^2 = 545$, $P < 0.0001$). In Streak-chested Antpittas, 53% of artificial nests were depredated, whereas 82.5% of real nests failed ($\chi^2 = 68.5$, $P < 0.0001$). Too few Bicolored Antbird nests were found to execute comparisons using CONTRAST. A simple comparison of numbers of artificial nests lost (2 of 12) versus real nests lost (2 of 7) suggested no significant difference (Fisher's exact test, $P = 0.47$), but daily predation rates of real Bicolored Antbird nests were nearly three times the daily predation rates of artificial Bicolored Antbird nests (2.6% vs. 0.9% day⁻¹). Losses of artificial and real Spotted Antbird nests were not significantly different ($\chi^2 = 0.18$, $P = 0.93$). Interestingly, damage to Spotted Antbird nests indicated that predators of artificial and real nests probably differed. Eight of 9 depredated artificial nests were torn, whereas 7 of 40 depredated real nests were torn. Of the seven damaged real nests, four had major damage (holes torn in the nest or bottom ripped out), and three had minor damage (tilted or with sides stretched). The occurrence of damage to artificial and real nests was significantly different (Fisher's exact test, $P = 0.0001$).

DISCUSSION

Predation on real and artificial nests was significantly different in two of the four species and differed by 50% in a third species. Real nests of Bicolored Antbirds and Streak-chested Antpittas were lost to predators about twice as often as artificial nests, whereas Checker-throated Antwren artificial nests were never depredated. For those three species, artificial nests underestimated real nest predation. In the case of Spotted Antbird nests, predation on real and artificial nests was statistically similar, but the condition of depredated nests differed. That difference suggests that real and artificial nests attracted different types of predators and that the similar predation rates occurred by chance. The possibility that different predators attack

FIG. 1. (left) Daily predation rates (mean \pm SE) for real nests of the four target species during the incubation stage in 1997, 1998, and 1999, and artificial nests in 1998. The four species were Bicolored Antbird (BCAB), Checker-throated Antwren (CTAW), Streak-chested Antpitta (SCAP), and Spotted Antbird (SPAB).

real and artificial nests was suggested by Wilson et al. (1998) and was confirmed recently during video studies in Missouri forests by Thompson and Burhans (2004).

Our comparison of predation on real and artificial nests was designed to maximize the chance that predation rates would be similar. Other studies comparing predation on real and artificial nests have used manmade nests or chicken (*Gallus domesticus*) eggs, simulated incubation periods of unnatural duration, or failed to show that artificial nests were placed in sites statistically similar to sites selected by real birds (Sloan et al. 1998, Wilson et al. 1998, Davison and Bollinger 2000). Our methodology should have improved the chances of our artificial nests of accurately estimating predation on real nests. The only exception was that we used *Coturnix* quail eggs, which are larger than the eggs of our study species. Nearly all artificial nest studies use eggs other than those from naturally occurring bird species, because it is logistically impossible or unethical to use eggs from wild bird species. Egg size can affect predation rates (Roper 1992; Haskell 1995a, b; Lindell 2000; Maier and DeGraaf 2000, 2001) if most nest predators are small-mouthed mammals unable to swallow or crack shells of larger eggs. We have no evidence that small-mouthed mammals are important predators at our study site. Instead, from the few predation events actually witnessed, most predators have been snakes or large birds (Robinson and Robinson 2001). On nearby Barro Colorado Island, video evidence of predation on real Spotted Antbird nests ($n = 10$) indicates that 80% of predation is by snakes and 20% by larger mammals, such as monkeys (*Cebus capucinus*) and coatimundis (*Nasua americana*; Robinson et al. 2005).

The observation that snakes are important predators on real bird nests is of particular importance because snakes rarely, if ever, eat cool *Coturnix* eggs (Roper 1992, Marini and Melo 1998, Buler and Hamilton 2000, Thompson and Burhans 2004). Measurement error resulting from that source of bias could be a reason why predation on artificial nests was less than predation on real nests at our study site. In the one species (Spotted Antbird) where predation on real and artificial nests was statistically similar but the condition of depredated nests varied, it is possible that snakes were the primary predators at real nests, whereas larger

mammals depredated the nests baited with quail eggs. Neither of the two Spotted Antbird nests depredated by snakes on Barro Colorado Island showed any sign of damage (Robinson et al. 2005).

We included data from real nests monitored the years before and after (1997 and 1999) our artificial nest study to portray how predation on artificial nests fits within the range of predation on real nests. A common justification researchers give for using artificial nests is that predation on artificial nests falls within the range of measurements of predation on real nests. Such comparisons often use data taken from years, sites, or habitats other than the ones in which a particular artificial nest study was conducted (Moore and Robinson 2004). Usually, the variation in predation on real nests is so wide that such comparisons are not especially informative. Our results indicate how misleading such comparisons can be. For example, in the case of Streak-chested Antpitta nests, artificial nest predation in 1998 was similar to predation on real nests in 1999; therefore, one could argue that predation on artificial nests could be used to successfully estimate predation on real nests. For such a comparison to be valid, one must assume that predator populations and all other factors influencing survival of bird nests are consistent among years. However, wide annual fluctuations in nest predation rates are well documented (Nice 1957, Nolan 1978).

An additional issue to consider is that artificial nests only estimate predation rates during incubation. Many bird species, perhaps especially in tropical forests, experience higher predation during the nestling phase, because adult activity around nests increases as nestling feeding trips increase (Martin et al. 2000). If predation risk is inconstant across the nesting cycle, error in predation risk estimation could be strongly influenced by this shortcoming of artificial nests. Our data illustrate that issue. Including losses of nests during both incubation and nestling phases, real Streak-chested Antpitta nests were lost to predators nearly three times as often as artificial nests ($\chi^2 = 147$, $P < 0.0001$; daily predation during nestling period: 0.259 ± 0.084 , $n = 7$). Loss of real Checker-throated Antwren nests doubled to $7.1 \pm 1.8\% \text{ day}^{-1}$ ($n = 28$) during the nestling phase. Bicolored Antbird nests failed nearly twice as often during the nestling ($4.7 \pm 3.2\% \text{ day}^{-1}$, $n = 5$) as during the incubation

phase ($2.6 \pm 1.8\%$ day⁻¹, $n = 7$). Predation on real Spotted Antbird nests was slightly higher during the nestling ($5.4 \pm 1.3\%$ day⁻¹, $n = 33$) than during the incubation phase ($4.4 \pm 0.8\%$ day⁻¹, $n = 55$). Therefore, drawing conclusions from measures of predation on artificial nests must also be tempered by realization that predation on real nests occurs during both incubation and nestling phases and that predation risk is not constant across those phases.

Given accumulating evidence that artificial nests do not accurately estimate predation on real nests (Moore and Robinson 2004), including the biases revealed by our and other comparative results (Roper 2003), conclusions drawn from artificial nest studies in the tropics should be viewed with skepticism. Unless they are rigorously demonstrated to be accurate estimators of nest predation rates, we recommend against the use of artificial nests in evaluating ecological hypotheses because of the many biases inherent to the method.

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