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# Experimental analysis of nest-sites and nest predation for a neotropical bird: stuck between a rock and a hard place

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RESUMO: **Análise experimental de locais de nidificação e predação nos ninhos de uma ave neotropical: entre a cruz e a espada.** A variação intraespecífica entre locais de nidificação e sua influência em sucesso reprodutivo, foram testadas experimentalmente. Em três anos seguidos ninhos e locais dos nidificação de *Thamnophilus punctatus* foram usados como modelos. O primeiro experimento no primeiro ano foi feito com ninhos naturais para testar se local influi na predação. Experimentos subseqüentes usaram locais semelhantes aos locais naturais e foram baseados no comportamento dos predadores para encontrar ninhos. A idéia era de que plantas em contato com as plantas de suporte dos ninhos oferecem mais caminhos de acesso predadores forrageando. Portanto, ninhos em plantas de suporte mais isoladas devem ter maior sucesso. Dois tratamentos foram usados: 1) plantas de suporte do ninho sem contato com outras plantas, e 2) plantas de suporte com mais de um contato (até muitos contatos) com outras plantas na área (no segundo ano, estes tratamentos eram emparelhados). Um terceiro experimento incluiu um tratamento de plantas suporte mais ainda isoladas, para as quais esperava-se obter o maior sucesso dos ninhos. Predação era a única causa de mortalidade dos ovos. Experimentos com ninhos naturais em locais naturais mostraram que o sucesso foi consistente entre réplicas repetidas, suportando a previsão que os locais influem na predação. Mas, em experimentos emparelhados, a sobrevivência foi melhor, igual, e menor nos ninhos isolados em cada um dos três anos, não suportando a idéia de que o isolamento das plantas seja importante. Por outro lado, os experimentos com três tratamentos apresentaram a ordem de sucesso antecipada nos dois anos deste experimento, suportando a previsão que isolamento é importante. Neste último experimento, porém, os tratamentos dentro de uma mesma réplica não eram independentes, ou seja, quando um ninho foi predado, os outros ninhos na réplica tinham maior probabilidade de serem predados também. Este padrão ocorreu devido ao fato dos ninhos mais isolados estarem distantes da vegetação, chamando a atenção de predadores que não são normalmente importantes no subbosque, mas que, chegando ao ninho isolado também encontraram os outros ninhos da réplica. Este padrão sugere que, apesar das altas taxas de predação em plantas não isoladas, os pássaros não tem opção de locais para colocar ninhos com menor probabilidade de predação, porque a opção mais sensata seria expor-se a um novo predador - os pássaros ficam entre a cruz e a espada.

PALAVRAS-CHAVES: organização de experimentos, aves neotropicais, predação dos ninhos, seleção de locais de nidificação, *Thamnophilus punctatus*.

ABSTRACT. Intraspecific nest-site variation and its influence on nesting success was examined experimentally. Nests, and nest-sites, of the slaty antshrike (*Thamnophilus punctatus*) were used as models. The first experiment used natural nests to test whether success is repeatable in nest sites, and each nest was its own replicate. Subsequent experiments used nests in sites similar to natural sites, and experimental logic was based on the prediction that predators use forest understory vegetation as foraging paths, and these paths should influence predation proportional to their abundance. That is, nest-support plants in contact with many adjacent plants (many avenues of travel for the predators) should be less successful due to greater predation. In paired experiments, two treatments were used: 1) nest-sites with no contact with nearby vegetation, and 2) nest-sites with few to many contacts with nearby vegetation. The third experiment added a treatment, more distant from nearby vegetation, which was predicted to be most successful. Only predation caused nest failure. In experiments with natural nests in natural sites, success was repeatable, supporting the prediction that sites influence predation. In paired experiments, daily survival rates were greater in the isolated nests in only the first year. The three-treatment experiment showed the predicted rank order of success occurred in both years (distant > isolated > contact). However, within replicate nest predation was no longer independent among treatments. That is, when one nest failed, the other nests failed more than expected. This was due to the third nest treatment (distant), either because novel predators were attracted to the third treatment, or old predators found the third treatment more easily, and upon finding it, found the other nests within the replicate. If these are novel predators, then the use of an apparently better nest site given normal predators may actually be less successful given new predators. I suggest that this pattern may explain why antshrikes do not use an otherwise better nest site, and so are constrained to nest in places that have consistently low success.

KEY WORDS: experiments, neotropical birds, nest predation, nest-site selection, *Thamnophilus punctatus*, novel predators, experimental design.

Nest predation is the main cause of reproductive failure for many passerine birds (Ricklefs 1969). This observation suggests that nest-site selection may be important to reduce predation risk. Nest-site selection and its influence on predation risk has received considerable attention (Oniki 1979, 1985, Zimmerman 1984, Skutch 1985, Wilcove 1985, Martin 1988, 1992, 1995, Martin and Roper 1988, Miller and Knight 1993, Norment 1993). Experiments show that nest sites may influence predation risk (Bowman and Harris 1980, Loiselle and Hoppes 1983, Martin 1989, Langen *et al.* 1991, Sieving 1992, Amarasekare 1993, Laurance *et al.* 1993, Rudnicky and Hunter 1993). Usually, ground nests experience different predation rates than above ground nests (Loiselle and Hoppes 1983, Wilcove 1985, Martin 1989), and vegetation near nests may influence predation probability (Bowman and Harris 1980, Yahner and Voytko 1989, Martin 1993). However, experiments use large differences in nest-sites for comparison, such as forest sites *versus* edge sites or sites in forest fragments (*e.g.*, Loiselle and Hoppes 1983, Wilcove 1985, Yahner and Scott 1988, Yahner *et al.* 1989, Nour *et al.* 1993, Rudnicky and Hunter 1993).

Intraspecific variation in nest-sites, if it influences predation rates, may have important fitness and, therefore, evolutionary consequences. Intraspecific variation in nest success can occasionally be attributed to vegetation characteristics of nest sites (Best 1978, Martin and Roper 1988, Marzluff 1988, Norment 1993). However, other studies do not find site influences on predation, even when predation rates are high (Holway 1991, Morton *et al.* 1993, Steele 1993, Crick *et al.* 1994, Filliater *et al.* 1994). This intraspecific aspect of nest-site selection has yet to be experimentally examined.

In the neotropics, where nest predation rates are often very high (Skutch 1985), experimental studies of nest predation are few (Loiselle and Hoppes 1983, Gibbs 1991, Roper 1992, Sieving 1992), and none examines the intraspecific influence of nest-sites on nest predation risk. Here I describe the first experimental study of the influence of intraspecific variation in nest-site quality on nesting success in a neotropical bird. I tested the predictions that: first, nest-sites influence nesting success for an individual species of neotropical understory bird; second, specific, identifiable vegetation characteristics of nest-sites influence predation rates for this species; and third, that birds are constrained by limited options in nest-site choice.

## METHODS

*Study Area and Species.* Experiments took place on Pipeline Road in central Panamá, in the *Parque Nacional Soberania.* Pipeline Road is an area of the park used exclusively for research and is relatively undisturbed. Experiments were carried out during the months of May to August in 1991 and 1992, throughout most of the year of 1993, and during May and June of 1994. Nest-sites for experiments were based on the nest sites of the Slaty Antshrike (*Thamnophilus punctatus*, Oniki 1975, Ridgley and Tudor 1994). Slaty antshrikes experience high predation rates (Roper 1992, Roper and Goldstein 1997), build cup nests in low shrubs in the forest understory, in a horizontal fork of a branch, one to five m in height (Oniki 1979). This experimental study area is within the areas in which Slaty Antshrikes naturally nest, and within the boundaries of approximately 30 territories that were part of a larger study. Nests are used once by antshrikes (J. Roper, unpublished data).

*Variation in Predation in Natural Nest-sites.* To test that predation risk differed among nest-sites, antshrike nests in their original sites were used in a preliminary experiment in 1991. This experiment was important because if the "consistent sites" prediction were rejected, then further study of site quality would be unnecessary. Seventy antshrike nests, no longer used by the birds, were used as experimental nests. A single coturnix quail egg was placed in each nest and checked on alternate days for 22 days or until nest failure (egg disappearance). One to three weeks later, the experiment was repeated in the same nests. Two results are required in this experiment to demonstrate that nest-sites vary in their influence on predation. First, nests should have similar outcomes in both trials. That is, the site must influence predation such that a nest in a good site should tend to succeed in both trials. To test this prediction, a 2x2 contingency table was used to compare success and failure on the first and second trials ($\alpha = 0.05$). Second, predation events in the second trial must be independent of those in the first trial. If predators returned to nests, then predation rates on the second trial should be greater than the first trial. To test this prediction, predation rates were compared between the first and second trials by the Mayfield method (Mayfield 1961, 1975, Hensler and Nichols 1981).

*Nest-site Characteristics – Moved Nests.* To test a specified nest-site characteristics, namely nest isolation, and its influence on predation, an experiment in two treatments was used. Small opossums (mostly) and snakes (occasionally) were known to be predators (Roper 1992, Roper and Goldstein 1997), and their foraging patterns provided the rational to examine nest-isolation. These animals may move through the understory without descending to the ground and pass from shrub to shrub in search of prey. Nests that could only be found if the predator ascended the trunk of the nest-shrub were predicted to be more successful than nests that could be found by several paths. Two experimental nest-site types reflecting these features were used. The first, "contact" nests, were in small shrubs whose branches were in contact with some (any number of branches greater than two) adjacent understory plants. The second, "isolated" nests, were in shrubs of which the branches did not touch any adjacent shrubs or branches of shrubs. Otherwise, the two nest-sites were similar, and either treatment could be in thick, nearby vegetation, and so hidden from view at a distance. In 1991, each nest was placed randomly in the study plots, never closer than 30 m to another replicate. In 1992, 1993 and 1994, nests were paired and both treatments were within 10 m of each other and replicates were at least 30 m apart. Pairing replicates avoids confounding local variation in predator abundance with nest-site quality.

An additional experiment in 1993 and 1994 included a third treatment. This third treatment ("distant") was in a shrub that was at least 3 m from any other vegetation yet still within 10 m of the other two treatments. Predators that travel and forage in and near understory vegetation should not often encounter these distant sites. Distant sites were predicted to be most successful because they are farthest from the predators foraging routes. The predicted rank order of nesting success in these experiments was "distant > isolated > contact".

All experimental nests followed the same protocol of egg placement and checking. One quail (*Coturnix coturnix*) egg was placed in all nests within replicates in both experiments. Eggs were obtained from markets in Panamá, and remained in their original box until placed in experimental nests. Eggs were carefully held with a freshly picked leaf from a nearby plant to avoid putting a human scent on eggs. Nests were checked on alternate days for 22 days or until nest failure. If any nest in any replicate was preyed upon then the other nests in that replicate were terminated but classed as successful. Thus each replicate could have from zero to all nests preyed on. To test the one-tailed hypothesis that contact nests failed more frequently than isolated nests, G-tests were used ($\alpha = 0.05$). Nests used in experiments were natural antshrike nests (in all years) and some wicker nests (in 1993 and 1994). Natural slaty antshrike nests were removed from the original site (by clipping branches) and tied with fine wire in sites selected as described above. Wicker nests were used to increase sample size. To test for a potential nest-type bias in the experiments, survival was compared among experimental natural nests in their natural location, moved natural nests, and wicker nests, also using the G-test and $\alpha = 0.05$.

Independence of predation risk among treatments within a replicate was a premise of these experiments. That is, to test the influence of sites, then predation on one nest in a replicate should not cause predation on other nests in the replicate. This was tested by calculating the probability of a nest failing in each treatment. The joint probability was calculated to determine the expected values of multiple nests failing within a replicate. The observed number of zero, one or two failures (or three in the three-treatment experiment) in a replicate was compared with the expected values (G-test, $\alpha = 0.05$).

## RESULTS

*Variation in Predation Among Natural Sites.* Natural, experimental nests that were successful in their first trial were more likely to be successful in the second trial ($G = 5.6$, $p < 0.02$, table 1). Daily survival rates did not change from the first to the second trial (first trial 0.94 day$^{-1}$ versus 0.95 day$^{-1}$, $z = 0.6$, $p > 0.2$) and so predators were unlikely to have learned to repeatedly visit nests. This first test supported the predicted nest-site influence on predation – good sites are consistently good.

*Nest-site Characteristics Experiments.* Isolated and contact nest treatments in the unpaired experiment in 1991 had similar success (11 of 29 nests versus 13 of 27 nests succeeded, respectively). This experiment did not control for local predator abundance (by paired treatments). When predator abundance was controlled in paired experiments, isolated paired nests were marginally more successful than contact nests only in 1992 ($G = 3.27$, $df = 1$, $p = 0.07$). Experiments in 1993 and 1994 had no treatment influence on nest-success (all $p > 0.10$, table 2).

Table 1. Successful and failed nests in two trials of repeated experiments on nest-site quality (1991). $G = 5.6$, $df = 1$, $p < 0.02$.

| First Trial | Second Trial | |
|---|---|---|
| | Successful | Unsuccessful |
| Successful | 11 | 8 |
| Unsuccessful | 14 | 37 |

Table 2. Successful and failed nests by treatment in experiments with two treatments.

| Year | Treatment | Successful | Failed | Daily Survival (a) | G |
|---|---|---|---|---|---|
| 1991(b) | Contact | 13 | 14 | 0.968 | 0.60 |
| | Isolated | 11 | 18 | 0.956 | |
| 1992 | Contact | 18 | 15 | 0.970 | 3.27* |
| | Isolated | 25 | 8 | 0.985* | |
| 1993 | Contact | 14 | 12 | 0.960 | 0.00 |
| | Isolated | 14 | 12 | 0.960 | |
| 1994 | Contact | 21 | 8 | 0.979 | 1.87 |
| | Isolated | 16 | 13 | 0.968 | |

a) Daily survival rates are Mayfield estimates shown for comparative purposes; b) in 1991 treatments were unpaired (paired in all subsequent years); *) in 1992 isolated nests were marginally more successful ($p = 0.071$ for G-test, $df = 1$; $p = 0.06$ for the Mayfield estimate).

Success in the three-treatment experiment was in the predicted rank order (distant > isolated > contact) in both 1993 and 1994 ($p < 0.03$). The calculated probability comes from the chances of obtaining the same ordering of three possibilities in two years. In each year, however, the trend was weak as measured by contingency tables or the Mayfield method (table 3). If only distant and contact treatments are compared by the Mayfield method, daily survival rates are greatest in distant nests ($p = 0.08$ in 1993, and $p = 0.03$ when years are pooled, table 3).

Table 3. Successful and failed nests by treatment in triad experiments.

| Year** | Treatment | Successful | Failed | Daily Survival | G |
|---|---|---|---|---|---|
| 1993 | Contact | 20 | 23 | 0.969 | 3.25 |
| | Isolated | 22 | 21 | 0.972 | |
| | Distant | 28 | 15 | 0.980* | |
| 1994 | Contact | 12 | 8 | 0.969 | 1.91 |
| | Isolated | 14 | 6 | 0.978 | |
| | Distant | 16 | 4 | 0.985* | |

*) Daily survival rates were greater on distant when compared with contact treatments summed over years ($p < 0.05$); **) within year differences were not significant. When years were pooled, $G = 4.91$, $df = 2$, $p = 0.086$.

All experimental nest types had similar daily survival rates. Slaty antshrike nests in their original location, with quail eggs, survived at the rate of 0.9636 day$^{-1}$, moved nests (pooled over all treatments) survived at 0.9706 day$^{-1}$, and wicker nests (also pooled) at 0.9714 day$^{-1}$. Mayfield comparisons of the experimental nest types were not significant (a difference of 0.0078 day$^{-1}$, $z = 1.397$, $p > 0.05$), supporting that no bias existed due to the type of experimental nest used.

Predation on any within-replicate nest was independent of predation on the other nest in the replicate in the paired experiments ($G = 0.0$, $df = 2$, $p > 0.3$, figure 1A). However, in the three-treatment experiments predation within a treatment was influenced by predation on other nests within that treatment. When the distant nest in a replicate was depredated, the probability of the other two nests being also preyed on was greater than expected ($G = 63.5$, $df = 3$, $p < 0.01$, figure 1B).

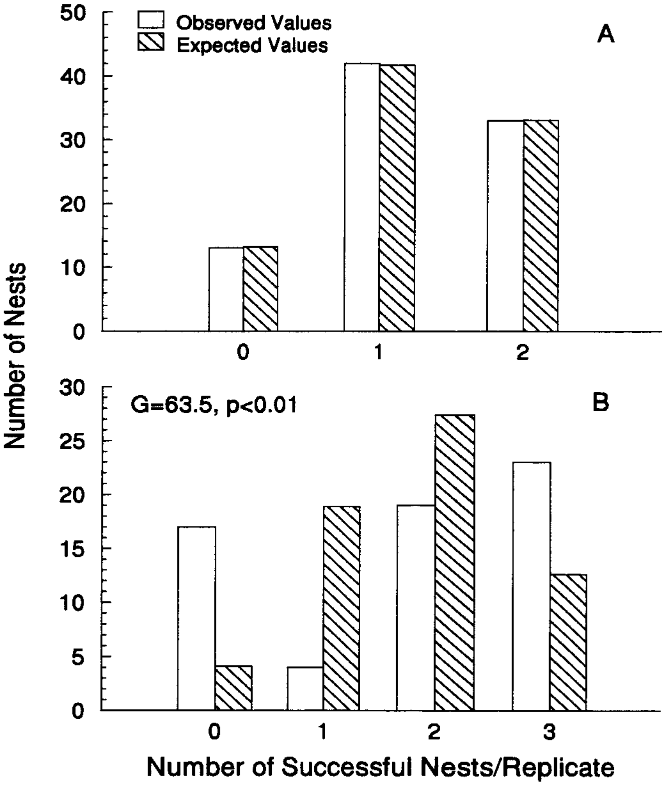

Figure 1. Comparisons of expected and observed numbers of successful nests in each replicate in the experiments with moved nests. A) Paired experiments, in which observed and expected values were nearly identical, and B) three-treatment experiments, in which the number of replicates with three successful nests was greater than expected, and the number of replicates with three unsuccessful nests was less than expected ($G = 63.5$, $p < 0.01$).

## DISCUSSION

Nest predation experiments usually demonstrate habitat or site differences in predation rates (Loiselle and Hoppes 1983, Yahner 1985, Yahner and Voytko 1989, Gibbs 1991, Langen *et al.* 1991, Laurance *et al.* 1993, Nour *et al.* 1993). However, most experiments examined broad, interspecific differences in nest-sites and their associated predation risk, or large among-habitat differences. Natural selection should act on nest-site selection of individual birds or pairs of birds. Experiments, if designed to address nest-site selection *per se*, should examine intraspecific variation in nest-site selection, and how such selection influences nest predation.

In this study, potentially conflicting results were found. The first experiment showed that within-nest success was repeatable and so supported the prediction that nest-sites influence predation risk. Paired experiments had equivocal support of the influence of nest sites. Finally, the three-treatment experiments again supported the prediction that nest-sites influenced predation. To understand these results, the experiments, their design and predators need to be discussed.

The first experiment supported the prediction that nest-sites may influence predation; that is, success at nests was consistent in repeated trials (table 1). However, this pattern can occur for at least two reasons. First, site quality itself (as predicted) can influence predation. Second, non-random spatial patterns of predator abundance could be an alternative explanation for apparent nest predation consistency. Mouse opossums, a common predator (Roper and Goldstein 1997), may show clumped distributions. But mammal population dynamics and distribution patterns are poorly known in the neotropics (Eisenberg 1989, Emmons 1990), and so this idea is only presented as one possible alternative to nest-site quality. On the other hand, if local variation in predator abundance occurs, and is consistent over time, then it may influence territory selection because birds that select territories with few predators should have greater reproductive success (Martin 1988). These alternatives to the nest-site quality hypothesis remain untested. Tests will require understanding population dynamics of the nest predators, which are still very poorly studied (Dunn 1949, Eisenberg 1989, Emmons 1990). A third reason for this result is not immediately evident, but includes the kinds of predators that are important at experimental nests. I will discuss this problem below while explaining the biases of the two-treatment experiments.

The two-treatment experiments did not support the prediction that contact vegetation provided avenues for predator travel, except in the first year they were paired (enough to motivate subsequent years of experiments, table 2). In the first, unpaired year, this result can also be explained by local predator abundance. The second year, when nests were paired, the results marginally supported the predicted influence of contact vegetation. Subsequent years showed no trends, however. In addition to local predator abundance, the type of predator can also account for these results. Experimental nests are known to be biased towards predators that can eat quail eggs (Roper 1992, DeGraaf and Maier 1996, Roper and Goldstein 1997). The main predator in this study is probably the mouse opossum, which is unable to eat quail eggs. These experiments, therefore, measure other, less important, predators. For example, Roper (1992) reported low nest success at approximately 0.91 day$^{-1}$; here experimental nest success was high at near 0.97 day$^{-1}$. Snakes may account for much of this relatively low predation rate. If so, then experiments are unable to address the problem of what predator is important from the perspective of the birds. Future experiments need to address this issue, if we wish for experiments to provide realism to experimental studies. The importance of understanding the predator is highlighted by considering the experiments with three nest treatments.

Experiments with three treatments, in contrast with the two-treatment experiments, supported the predicted trends in rank order of nest success. Also, Mayfield estimates of daily survival rates showed that distant nests were more successful than contact nests (table 3). Here, contrary to the previous results, nest-sites influenced predation. Understanding this pattern provides a hypothesis for why birds do not choose better sites. In the paired nests experiments, success of one nest within a replicate was independent of that of the other nest. In three-treatment experiments nest predation was no longer independent among nest treatments within a replicate. When the new, distant, treatment was preyed upon, the probability of predation at the other two treatments increased.

In paired experiments, the "isolated" treatment was often hidden by nearby plants and was seldom visible at a distance. The "distant" treatment, on the other hand, was more exposed because of the minimum distance to nearby vegetation and was often visible at larger distances than the other two treatments, especially from above. Therefore, this nest treatment was more easily encountered if the predator was a visually hunting and diurnal predator. This treatment, while less likely to be found by the common natural predators, possibly became accessible to new predators, or more easily found by the common natural predators. Once the predator found the distant nest treatment, then finding the other nearby treatments was perhaps facilitated. A variety of potential predators may fit this scenario (monkeys, birds such as raptors and toucans).

The possibility that potentially high quality nest sites based on normal predators are instead low quality sites because of new predators has potentially important consequences for experimental studies as well as for understanding natural processes. As we have seen, experiments are biased away from the important small predators, such as mouse opossums. The predicted pattern of isolation and nest success may be correct in natural nests but experiments are unable to show it because small natural predators cannot eat quail eggs (Roper 1992, DeGraaf and Maier 1996). If so, and if birds attempting to select isolated sites choose sites that are too isolated, such as the distant treatment, then the birds may then become exposed to new predators. Antshrikes appear to prefer sites with fewer contacts: the number of branches in contact with shrubs in which antshrikes nests varies from none to 50 or more, with many more nests in sites with fewer contacts (J. Roper unpublished data, figure 2). Testing whether antshrikes select nests with fewer contacts would require some estimation of the distribution of branches in contact with suitable but random nest shrubs found in suitable habitat, which is not a simple proposition. While the tendency may be for antshrike to choose nest sites with few contacts, too much isolation could also be detrimental.

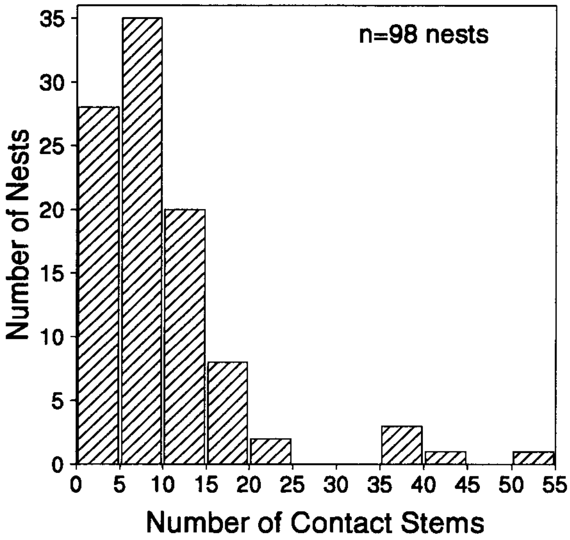

Figure 2. Frequency distribution at 98 Slaty Antshrike nests of the number of stems of adjacent shrubs in contact with the nest shrub, excluding one outlier with 180 contact stems.

These experiments illustrate several issues that are seldom addressed in experimental studies of nest predation and nest-site selection. Nest predation experiments may not have the resolution required to address the problem of nest-site selection due to biases associated with experiments. Nest types used in experiments may have no influence on predation, and experimental nests may need not mimic natural nests to test some hypotheses. Next, nest predation may be poorly influenced by nest-site selection within the range of sites birds use. In some scenarios in which the cause of nest failure can be identified, birds may nest to avoid those causes (Marzluff 1988). However, in a tropical scenario, where predators may be common and generalist foragers that prey on nests when encountered, the influence of nest-sites on predation may be tenuous, and all birds choose sites similarly. On the other hand, the three-treatment experiments showed that subtle differences in nest-sites may favor new predators, and so may explain why birds do not use these sites. Birds are unable to move to better sites to avoid their normal predators, because those potentially better sites may be accessible to new and possibly efficient predators - so Slaty Antshrikes are stuck between a rock and a hard place.

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