

# What do artificial nests tells us about nest predation?

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## Abstract

Artificial nests are commonly used to evaluate predation, but the assumption that this method mimics predation on natural nests has seldom been tested. Natural and artificial nests of eastern yellow robins (*Eopsaltria australis*) were monitored in four, 55-ha plots over two breeding seasons. Overall, daily survival rates were higher ( $P < 0.001$ ) for natural (95%/day) than for artificial nests (88%/day). Among plots, daily survival rates for the two types of nests were not correlated with one another ( $P = 0.72$ ) indicating that the spatial pattern of predation on artificial nests did not mimic that for natural nests. Seasonal variation was evident for natural nests in one year, when they were more successful at the beginning and end of the breeding season. No seasonal patterns were observed for artificial nests in either year. Neither natural nor artificial nests showed annual variation in predation. Previous researchers concluded that large birds were important predators on robin nests. In this study, predation by large birds on artificial nests was positively correlated with the numbers of large birds counted on the plots ( $P = 0.04$ ). However, large birds depredated only 16% of artificial nests. Daily survival rates for artificial nests were recalculated using predation by large birds only. These rates were compared with natural nests, but there was still no correspondence in the spatial and temporal patterns of predation for the two types of nests. These results suggest that inferences about predation on natural nests based on artificial nest studies should be avoided. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Predation is the primary proximate cause of nest failure for many avian species (Ricklefs, 1969). Investigations of nest predation have commonly used artificial nests containing eggs that are commercially obtained [e.g. Japanese quail (*Coturnix japonica*)] or synthetic eggs manufactured by the researcher (e.g. plasticine, wax etc.; reviewed in Major and Kendal, 1996). The absolute rates of predation on artificial nests have always been suspected of being different from natural nests (Wilcove, 1985), and this has been confirmed by some studies (Ortega et al., 1998; Sloan et al., 1998; Wilson et al., 1998). However, it is often assumed that both types of nests exhibit the same relative rates of nest predation over space and time. For example, if artificial nests are depredated faster in small than large forest fragments, it is generally assumed that predation on

natural nests also will follow this spatial pattern (Wilcove, 1985; Andrén and Angelstam, 1988; Arango-Vélez and Kattan, 1997). In fact, researchers often cite artificial nest studies as evidence that nest predation for songbirds is high along forest edges and in small forest fragments (reviewed in Paton, 1994). Many have questioned this assumption (Tellería and Santos, 1992; Haskell, 1995a; Hanski et al., 1996), but few have monitored the performance of artificial and natural songbird nests simultaneously over several sites, months, and years to compare the spatial-temporal patterns of predation for each type of nest. Such studies would make it possible to determine how well these two methods mimic each other.

Many potential biases are associated with the use of artificial nests. One example is that artificial nests may attract different types of nest predators than natural nests. Willebrand and Marström (1988) showed that while eggs in Eurasian black-grouse (*Tetrao tetrix*) nests were depredated mainly by mammals, birds took the majority of eggs in artificial nests. Haskell (1995a, b) suggested that while small-mouthed mammals such as

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eastern chipmunks (*Tamias striatus*) are important predators of bird nests, they are unable to break the shells of Japanese quail eggs placed in artificial nests. Thus, to understand predator pressure on artificial and natural nests, it is necessary to identify the main predators involved.

In this study, I calculated the nesting success of a forest songbird, the eastern yellow robin (*Eopsaltria australis*; hereafter “robin”), over 2 years in four study plots that were situated in two small and two large forest fragments in an agricultural landscape. Artificial nest experiments were conducted concurrently on the same plots. In a previous paper, Zanette and Jenkins (2000) found that predation rates did not vary with fragment size for either natural or artificial nests. In this paper, I am not considering fragment size. Instead, my intention is to determine how well predation rates for natural and artificial nests match spatially (i.e. across the four plots, irrespective of fragment size) and temporally. I predicted that while natural and artificial nests would be depredated at different absolute rates, the relative patterns of predation, across plots, months and years, would be similar. I also determined which predators preyed upon synthetic eggs in artificial nests. Zanette and Jenkins (2000) concluded that large birds (> 39 cm in length) were the principal predators on robin nests, so I expected most artificial nests to be depredated by large birds. Finally, I determined whether predation on artificial nests by large birds was positively related to their abundances and species richness.

## 2. Study area

I worked in temperate, northeastern New South Wales, Australia (30° 27' S 151° 13' E), from August to December 1995 and 1996. The original forest in this region has largely been converted into pasture for sheep and cattle grazing, so that today only 20% of the forest remains in patches of various sizes (Barrett, 1995). I worked in four, 55-ha study plots located in four different forest fragments. The plots were marked at 100-m intervals, and were located in two small fragments (55 ha in size; termed S1 and S2) and two large fragments (> 400 ha; termed L1 and L2). Vegetation in all plots was similar. Further details of the study area and plots can be found in Zanette et al. (2000) and Zanette and Jenkins (2000).

## 3. Methods

### 3.1. Robin nests

Robins are a multibrooded species that generally breed from August–December. Most of their open-cup

nests are built from 0.2–3 m above ground (median nest height = 1.75 m; Marchant, 1984, 1986), with two-egg clutches predominating (Zanette et al., 2000). I monitored all robin pairs that nested in the four study plots for the entire breeding seasons of 1995 and 1996. At least one member of each pair was colour banded for individual recognition. Nests were checked mainly at 1–2 day intervals (range 1–10 days), and the nesting period was 29 days, including 1 day pre-incubation, 16 days incubation, and a 12-day brooding period. In these populations, daily survival rates of nests do not vary between the egg and nestling stages (Zanette and Jenkins, 2000). I considered that a robin nest failed from predation when the entire contents were removed or when a nest was abandoned after partial predation. Robins almost always abandon a nest in which the clutch has been reduced in size to one egg. A successful nest fledged young. Fledging was confirmed when begging calls were heard and when parents were observed with food.

### 3.2. Artificial nests

To increase the chances that artificial nests would mimic the pattern of predation observed for natural nests, artificial nests and eggs were made to resemble those of robins. Tennis balls were cut in half, tree bark was glued to all surfaces, and the outside was decorated with lichen and moss. I made robin-sized eggs (22×16 mm, Slater et al., 1997) after mixing green, white and brown plasticine. A thin coating of varnish was applied and the eggs were speckled with rufous paint.

I conducted the artificial nest experiment monthly from September to November in 1995, and August to December in 1996. Two plasticine eggs were fastened into each nest with glue and twine (following Zanette and Jenkins, 2000). Fifteen artificial nests were distributed per plot along grid lines separated by 200 m. Nests were placed along each line every 200 m in 1995, and every 100 m in 1996 to reduce labour. To distribute nests, I went to pre-assigned grid markers and paced a minimum of 5 m NW, NE, SW, or SE, randomly assigned. Nests were securely fastened to tree forks or bushes using cable ties (28.6 cm long) threaded through two small holes drilled into one side of the artificial nests. Nests were placed between 0.2 and 2 m above the ground, well within the height range typically used by robins. No attempt was made to conceal nests. Robin nests generally are not concealed in vegetation (Marchant, 1986) and I wanted to avoid potential biases in nest predation across plots due to differences in concealment effort. Artificial nests were checked on days 3, 6, 9, and 16. A nest was considered depredated if one or both of the plasticine eggs were pecked or chewed. Depredated nests were removed from the field to avoid the possibility of further predation.

Predation was attributed to either birds or mammals based on imprints in the plasticine eggs. Subsequently, different size classes within each group were identified by comparing with museum specimens. Bill marks were categorized as being made by small- (8.5–20 cm, head to tail), medium- (21–36 cm), or large-sized birds (> 39 cm; sizes derived from Slater et al., 1997). The one exception was the medium-sized grey butcherbird (*Craicticus torquatus*), which is 30 cm long, but was categorized as a large bird because its bill leaves an imprint characteristic of large birds. Fine tooth marks were ascribed to house mice (*Mus musculus*) and large tooth marks to common brushtail possums (*Trichosurus vulpecula*).

I determined whether predation on artificial nests by large birds was associated with their abundances and species richness as measured in bird surveys (similar analyses for robin nests can be found in Zanette and Jenkins, 2000). Each study plot was surveyed once per month between September–November 1995 and August–December 1996. For each trial, after distributing the artificial nests, I conducted one survey per plot over four consecutive days, weather permitting. A bird survey occurred between 06:00 and 09:30 h and it consisted of five transect lines (each 200 m long and 50 m wide), 200 m apart. Within each year, the same transects were sampled each month but a different set of transects were sampled between 1995 and 1996.

All birds counted were categorized as small (8.5–20 cm), medium (21–36 cm), or large (> 39 cm). Large birds were further divided into potential nest predators [pied currawongs (*Strepera graculina*), laughing kookaburras (*Dacelo novaeguineae*), grey butcherbirds, Australian ravens (*Corvus coronoides*), and Australian magpies (*Gymnorhina tibicen*)], and other [e.g. galahs (*Eolophus roseicapilla*), Australian king parrots (*Alisterus scapularis*)].

### 3.3. Data analyses

For each type of nest, I calculated daily survival rates (DSRs) using the maximum likelihood estimator which corrects for the length of the interval between nest checks (Bart and Robson, 1982; Krebs, 1999). Standard errors were calculated following Bart and Robson (1982, equation 11). All comparisons of DSRs were made with program CONTRAST (Hines and Sauer, 1989). I tested for similarity in spatial patterns in nest survival using Pearson correlation coefficients. The sample size for each correlation test was eight because I calculated one DSR for each study plot in each year. These data were arcsine transformed to approximate a normal distribution.

I used log-linear analysis to determine whether the proportion of artificial nests depredated by small-, medium-, and large-sized birds was independent of study plot and year (3×4×2 contingency table; StatSoft

Inc., 1995). I determined whether predation on artificial nests by birds of different sizes was related to bird abundances and species richness, using Pearson correlation coefficients ( $n=8$  for all comparisons) on data that were square-root transformed to approach a normal distribution.

## 4. Results

### 4.1. Patterns of nest survival

Between 1995 and 1996, I found 282 natural robin nests and distributed 461 artificial nests in the four study plots. Fifteen robin nests (5%) failed for reasons other than predation, and 14 (3%) artificial nests had uncertain fates and were not used in analyses.

Survival was always higher for natural than for artificial nests (Table 1). The DSRs for natural versus artificial nests differed when examining each plot separately ( $P \leq 0.025$  in each year, and with years combined) with only one exception (i.e. the L1 plot: 1995,  $\chi^2_1 = 0.2$ ,  $P = 0.69$ ; 1996,  $\chi^2_1 = 4.7$ ,  $P = 0.031$ ; 1995–1996,  $\chi^2_1 = 3.4$ ,  $P = 0.067$ ). The DSRs for the two types of nests differed

Table 1  
Daily survival rates (DSR ± S.E.) for natural and artificial nests in four forest fragments (S1–L2) in 1995, 1996, and years combined<sup>a</sup>

	1995		1996		1995–1996	
	DSR	S.E.	DSR	S.E.	DSR	S.E.
<i>S1</i>						
Natural	0.914	0.012	0.940	0.010	0.927	0.008
Artificial	0.857	0.023	0.878	0.015	0.871	0.013
Artificial-Large	0.932	0.018	0.979	0.007	0.963	0.008
<i>S2</i>						
Natural	0.968	0.007	0.962	0.008	0.966	0.005
Artificial	0.901	0.017	0.873	0.015	0.885	0.011
Artificial-Large	0.988	0.007	0.992	0.005	0.990	0.004
<i>L1</i>						
Natural	0.913	0.018	0.923	0.019	0.917	0.013
Artificial	0.903	0.016	0.871	0.016	0.885	0.012
Artificial-Large	0.982	0.008	0.980	0.008	0.981	0.006
<i>L2</i>						
Natural	0.946	0.011	0.950	0.011	0.948	0.008
Artificial	0.861	0.022	0.869	0.016	0.868	0.013
Artificial-Large	0.948	0.016	0.980	0.008	0.968	0.008
<i>Overall</i>						
Natural	0.941	0.005	0.949	0.005	0.945	0.004
Artificial	0.885	0.010	0.873	0.009	0.878	0.006
Artificial-Large	0.965	0.006	0.983	0.004	0.976	0.003

<sup>a</sup> The values for “Natural” and “Artificial” nests were calculated based on the number of nests at risk of predation relative to those depredated (Krebs, 1999). For “Artificial-Large”, I used the number of nests at risk of predation relative to those depredated by large birds only.

also when all plots were combined ( $P < 0.001$  in each year, and with years combined).

Contrary to expectation, the spatial pattern of predation differed according to nest type (Pearson Correlation Coefficient,  $r = 0.2$ ;  $P = 0.72$ ). Although the DSRs for natural nests varied significantly across plots (1995,  $\chi^2_3 = 20.6$ ,  $P < 0.001$ ; 1996,  $\chi^2_3 = 5.5$ ,  $P = 0.14$ ; 1995–1996,  $\chi^2_3 = 24.6$ ,  $P < 0.001$ , Table 1), the same was not the case for artificial nests (1995,  $\chi^2_3 = 4.9$ ,  $P = 0.18$ ; 1996,  $\chi^2_3 = 1.9$ ,  $P = 0.98$ ; 1995–1996,  $\chi^2_3 = 1.6$ ,  $P = 0.66$ , Table 1). As for temporal patterns, seasonal changes in the DSRs were evident for natural nests in 1996 (1995,  $\chi^2_4 = 4.2$ ,  $P = 0.37$ ; 1996,  $\chi^2_4 = 16.4$ ,  $P = 0.003$ , Table 2) but not for artificial nests in either year (1995,  $\chi^2_2 = 4.6$ ,  $P = 0.10$ ; 1996,  $\chi^2_4 = 4.9$ ,  $P = 0.30$ , Table 2). In 1996, survival of natural nests was best in August and December. I found no differences in the DSRs between years for either natural ( $\chi^2_1 = 1.0$ ,  $P = 0.32$ ) or artificial nests ( $\chi^2_1 = 0.9$ ,  $P = 0.87$ ; Table 1).

#### 4.2. Nest predators

I identified the predators of 363 artificial nests. Of these, 99% were avian and 1% were mammalian. Two mammalian predators were common brushtail possums, and the third a house mouse. Among the avian predators, I classified 353/360 into the 3 size categories. Of these, 59.5% ( $n = 210$ ) were small, 24.1% ( $n = 85$ ) medium, and 16.4% ( $n = 58$ ) large predators.

Considering only avian predators, log-linear analysis revealed differences among the size categories when comparing plots ( $\chi^2_6 = 14.6$ ,  $P = 0.02$ ), and years ( $\chi^2_3 = 17.7$ ;  $P < 0.001$ ), with no three-way interaction ( $\chi^2_6 = 6.8$ ;  $P = 0.34$ ). Predation by large birds was between 1.4 to 3.5 times more frequent in S1 and L2 (23% of 94 and 21% of 85, respectively) than S2 and L1 (7% of 90 and 14% of 84, respectively), and over twice as frequent in 1995 as in 1996 (26% of 124 and 11% of 229).

The densities of large avian predators counted in the plots ranged from 0.08–0.56 birds/ha. I found a significant and positive correlation between large bird abundances and predation on artificial nests by large birds ( $r = 0.72$ ;  $P = 0.04$ ). Predation by small- ( $r = 0.48$ ;

$P = 0.23$ ) and medium-sized birds ( $r = 0.39$ ;  $P = 0.34$ ) was not associated with their relative abundances. In addition, species richness of small birds ( $r = 0.06$ ;  $P = 0.88$ ), medium birds ( $r = 0.29$ ;  $P = 0.48$ ), and avian nest predators ( $r = 0.26$ ;  $P = 0.54$ ) did not account for the amount of predation attributed to each of these groups.

A correspondence in the spatial and temporal patterns of predation between natural and artificial nests could have been masked simply because large birds have been identified as important predators on robin nests (Zanette and Jenkins, 2000), while most artificial nests were depredated by small birds. Therefore, I re-calculated the DSRs for artificial nests using data from large bird predation only (all other predation events were right-censored; Kleinbaum, 1996), and reanalyzed the data as in Section 4.1. Data for natural nests were not altered. I anticipated a significant correspondence in the relative DSRs for the two types of nests, although I expected no improvement in the absolute rates of predation.

In all cases, the absolute rates of predation for natural nests were lower than for artificial ones (Table 1). The DSRs for natural versus artificial nests were not comparable within most of the plots ( $P \leq 0.03$  in each year, and with years combined, Table 1). The exceptions were S1 in 1995 ( $\chi^2_1 = 0.7$ ,  $P = 0.40$ ), L2 in 1995 ( $\chi^2_1 = 0.0$ ;  $P = 0.95$ ), and L2 with years pooled ( $\chi^2_1 = 3.1$ ;  $P = 0.08$ ). DSRs for natural versus artificial nests also were not comparable when plots were combined ( $P \leq 0.003$  in each year, and with years pooled).

The DSRs for natural nests and the re-calculated DSRs for artificial nests exhibited different spatial patterns ( $r = 0.5$ ;  $P = 0.19$ ). The DSRs for artificial nests differed among the plots (1995,  $\chi^2_3 = 13.2$ ,  $P = 0.004$ ; 1996,  $\chi^2_3 = 3.5$ ,  $P = 0.33$ ; 1995–1996,  $\chi^2_3 = 13.9$ ,  $P = 0.003$ ) which is consistent with what I found for natural nests. However, while the survival of artificial nests was highest in S2 and L1, the survival of natural nests was highest in S2 and L2 (Table 1). Also, unlike natural nests, survival for artificial nests varied between years, being higher in 1996 ( $\chi^2_1 = 6.3$ ;  $P = 0.01$ ; Table 1). I was unable to examine seasonal effects of predation on artificial nests by large birds due to inadequate sample sizes.

Table 2

Seasonal changes in average daily survival rates (DSR  $\pm$  S.E.) for natural and artificial nests from 1995 and 1996

	Natural nests				Artificial nests			
	1995		1996		1995		1996	
	DSR	S.E.	DSR	S.E.	DSR	S.E.	DSR	S.E.
August	0.928	0.014	0.975	0.007			0.895	0.016
September	0.942	0.012	0.930	0.017	0.865	0.020	0.884	0.016
October	0.939	0.013	0.939	0.012	0.873	0.017	0.868	0.018
November	0.934	0.011	0.930	0.014	0.909	0.014	0.846	0.019
December	0.961	0.011	0.951	0.013			0.861	0.019

## 5. Discussion

In a previous paper, Zanette and Jenkins (2000) found that predation rates did not vary with fragment size for either robin or artificial nests. Furthermore, the abundances of large birds on the study plots were correlated with the DSRs of artificial nests. Researchers often compare the densities of potential nest predators with predation rates on artificial nests as a means of identifying important predators on natural nests (e.g. Andr en, 1992; M oller, 1989; Marini et al., 1995). Consistent with this idea, Zanette and Jenkins (2000) concluded that large birds were the principal predator of robin nests. Given that these two sets of results corresponded with one another, one could conclude that artificial nests were adequately mimicking predator pressure on robin nests and that the important predators on artificial and robin nests were similar (Matthews et al., 1999). The results from the current study, however, showed that these conclusions are not valid. My results indicated that with few exceptions, the absolute rates of predation on artificial and natural nests differed. When I considered all predation events, artificial nests were depredated about twice as fast as natural nests (for similar results see Sloan et al., 1998). When the DSRs of artificial nests were calculated based on predation by large birds only, I again found differences in survival rates with nest type. In this case, natural nests were the ones depredated at a faster rate (Willebrand and Marcstr om, 1988). In neither case did the spatial pattern of predation correspond between natural and artificial nests. Thus, both the absolute and relative rates of predation varied depending on nest type. I also did not find consistent seasonal or annual patterns of predation between the two types of nests. Finally, artificial and natural nests attracted different predators (Willebrand and Marcstr om, 1988; Sloan et al., 1998) since most artificial nests were depredated by small birds.

Differences in the absolute rates of predation between artificial and natural nests could be due to differences in nest appearance (Martin, 1987), nest height (Ortega et al., 1998) egg colour (Yahner and Mahan, 1996), egg size (Haskell, 1995b), and concealment (Leimgruber et al., 1994). In my study, artificial nests and eggs closely resembled those of robins, and were placed at heights typical of robin nests. Although I have no quantitative data on concealment for artificial nests, most studies have reported no significant influence of concealment on the survival of artificial nests (Gottfried and Thompson, 1978; Yahner and Voytko, 1989; Reitsma et al., 1990; Hanski et al., 1996; Bayne and Hobson, 1997; but see Leimgruber et al., 1994). Concealment had no effect on the nesting success of robins (Zanette and Jenkins, 2000).

Many other explanations for differences in the absolute rates of predation between artificial and natural

nests have been proposed, but few common patterns have emerged from the literature. For example, the absence of parental activity at artificial nests may deter (Rudnicki and Hunter, 1993) or attract (Skutch, 1985) nest predators. Similarly, artificial nests are uncovered and unguarded by parents which could render them either more or less prone to predation (Yahner et al., 1989; Martin, 1992). Human visitation rates at nests may (Major, 1990) or may not (Gottfried and Thompson, 1978; MacIvor et al., 1990; Zanette and Jenkins, 2000) increase predation. Human scent or other odours (e.g. glue) on artificial nests may attract (Willebrand and Marcstr om, 1988; Sloan et al., 1998), deter (MacIvor et al., 1990), or have no effect (reviewed in G tmark, 1992; Ortega et al., 1997) on predation rates by mammals.

Finding that artificial and natural nests suffer different absolute rates of predation is not surprising, and it does not mean that artificial nests are not useful in assessing how predation varies across space and time. In fact, if the spatial or temporal patterns of predation on artificial nests parallel that found for natural nests, then artificial nests would be a very useful tool. The assumption made when artificial nests are used or when evidence from artificial nest studies is cited is that relative predator pressure is similar for both nest types. My results do not support this assumption. I found no correspondence between the survival rates for the two types of nests. Furthermore, the artificial nests did not show the same within-year seasonal changes in predation rates observed for robin nests in 1996. Few have examined predation on natural and artificial nests simultaneously to compare spatial and seasonal patterns. Ammon and Stacey (1997) found higher predation on both songbird and artificial nests in grazed compared to ungrazed riparian zones. Sloan et al. (1998) found seasonal changes in predation on artificial nests in unbroken forests in New Hampshire but they did not compare them with breeding songbirds.

I have shown that predation rates on artificial nests did not correspond to those for robin nests, and that artificial nests were poor mimics of the spatial-temporal patterns of predation detected for robin nests. In addition to these biases, I found that 84% of artificial nests were pecked by small- and medium-sized birds, while only 16% were pecked by large avian species, the anticipated predator. My findings for smaller birds suggest either that small birds regularly depredate artificial nests but not natural nests, or that small birds routinely depredate both types of nests. In the latter case, the contributions of small birds to the failure of natural nests would have to be much greater than previously presumed.

Smaller birds do prey upon the eggs of robins, but robins can successfully chase smaller birds from the nest site (Zanette, 1997). To estimate the degree of damage that smaller birds may inflict upon robin nests, I calcu-

lated the percentage of nests that contained damaged eggs or suffered from partial clutch loss. These two criteria were used because, unlike larger species, small birds puncture eggs and consume their contents directly in the nests of robins (Zanette, 1997). If small birds only have time to puncture the egg-shell before they are deterred by the female, then the damaged egg is left in the nest but the rectangular hole left in the egg-shell is quite distinctive (Zanette, 1997). On the other hand, if the contents of the damaged egg are consumed, the incubating female will remove the empty egg-shell from the nest upon her return, resulting in partial clutch loss. In total, 10.8% (19/176) of robin nests suffered partial clutch loss or contained damaged eggs (L. Zanette, unpublished data), a much lower estimate than suggested by the artificial nest experiment. Thus, it would appear that most artificial nests were depredated by predators unlikely to cause much damage to natural nests. Other artificial nest studies have suffered from a similar problem (Willebrand and Marström, 1988; Haskell, 1995a; Sloan et al., 1998; Wilson et al., 1998).

Another possibility, however, is that predators on artificial nests were not accurately identified. Major et al. (1996) found that 13% of large birds produced marks on plasticine eggs consistent with small birds, while 19% of small birds produced damage characteristic of large birds. If these percentages were to apply in my study, then predation by small birds would *increase* by 6% (89% overall) while predation by large birds would be reduced by 6% (10% large birds predation overall).

## 6. Conservation implications

My study showed that the artificial nest technique that I used suffered from potential biases because neither predation rates nor the spatial-temporal pattern of predation for artificial and robin nests corresponded with one another. Furthermore, the vast majority of artificial nests in my study were depredated by smaller birds, which probably have little impact on the survival of natural nests. Thus, artificial nests gave me little insight as to the identity of the main predators on robin nests. Given my results, I recommend that artificial nests not be used as a substitute for measuring the survival of songbird nests. Although many have previously cautioned against artificial nests (reviewed in Major and Kendal, 1996), my results provide evidence that this warning is well-founded.

Nest predation is often cited as a primary cause for poor songbird reproduction in fragmented landscapes (Wilcove, 1985; Angelstam, 1986; Andrén and Angelstam, 1988; Temple and Cary, 1988; Robinson et al., 1995), and recommendations to manage nest predators based on this assumption have been made. Yet, this

conclusion is based principally on studies that have used artificial nests rather than studies on real birds (reviewed in Paton, 1994). To get a better understanding of how and whether predator pressure on songbird nests changes in fragmented landscapes, my results show that natural nests must be used. In fact, the poor correspondence in predators and predator pressure between artificial and natural nests in this study indicates that this long-standing conclusion must be reevaluated. Consequently, I would advise that researchers refrain from drawing conclusions about the importance of nest predation based on artificial nest studies. Studying natural nests is more time consuming and labour intensive, but the information obtained will be more reliable and ultimately more useful for conservation.

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## References

- Ammon, E.M., Stacey, P.B., 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. *Condor* 99, 7–13.
- Andrén, H., 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73, 794–804.
- Andrén, H., Angelstam, P., 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69, 544–547.
- Angelstam, P., 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47, 365–373.
- Arango-Vélez, N., Kattan, G.H., 1997. Effects of forest fragmentation on experimental nest predation in Andean cloud forest. *Biological Conservation* 81, 137–143.
- Barrett, G.W., 1995. Woodland bird assemblages on the New England Tablelands, Northeastern New South Wales. Dissertation, University of New England, Armidale, New South Wales, Australia.
- Bart, J., Robson, D.S., 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63, 1078–1090.
- Bayne, E.M., Hobson, K.A., 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11, 1418–1429.
- Götmark, F., 1992. The effects of investigator disturbance on nesting birds. In: Power, D.M. (Ed.), *Current Ornithology*, Vol. 9. Plenum Press, New York, USA, pp. 63–104.

- Gottfried, B.M., Thompson, C.F., 1978. Experimental analysis of nest predation in an old-field habitat. *Auk* 95, 304–312.
- Hanski, I.K., Fenske, T.J., Niemi, G.J., 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *Auk* 113, 578–585.
- Haskell, D.G., 1995a. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* 9, 1316–1318.
- Haskell, D.G., 1995b. Forest fragmentation and nest predation: are experiments with Japanese quail eggs misleading? *Auk* 112, 767–770.
- Hines, J.E., Sauer, F.R., 1989. Program CONTRAST: A General Program for the Analysis of Several Survival or Recovery Rate Estimates (US Fish and Wildlife Service Technical Report 24).
- Kleinbaum, D.G., 1996. *Survival Analysis: A Self-learning Text*. Springer, New York.
- Krebs, C.J., 1999. *Ecological Methodology*, 2nd Edition. Benjamin/Cummings, Menlo Park, California.
- Leimgruber, P.W., McShea, J., Rappole, J.H., 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58, 254–260.
- MacIvor, L.H., Melvin, S.M., Griffin, C.R., 1990. Effects of research activity on piping plover nest predation. *Journal of Wildlife Management* 54, 443–447.
- Major, R.E., 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132, 608–611.
- Major, R.E., Kendal, C.E., 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138, 298–307.
- Major, R.E., Gowing, G., Kendal, C.E., 1996. Nest predation in Australian urban environments and the role of the pied currawong, *Strepera graculina*. *Australian Journal of Ecology* 21, 399–409.
- Marchant, S., 1984. Nest-records of the eastern yellow robin, *Eopsaltria australis*. *Emu* 84, 167–174.
- Marchant, S., 1986. Breeding of the eastern yellow robin, *Eopsaltria australis*. In: Keast, A., Recher, H.F., Ford, H.A., Saunders, D. (Eds.), *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management*. Royal Australasian Ornithologists Union and Surrey Beatty & Sons, Sydney, Australia, pp. 231–240.
- Marini, M.A., Robinson, S.K., Heske, E.J., 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biological Conservation* 74, 203–213.
- Martin, T.E., 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor* 89, 925–928.
- Martin, T.E., 1992. Interaction of nest predation and food limitation in reproductive strategies. In: Power, D.M. (Ed.), *Current Ornithology*, Vol. 9. Plenum Press, New York, USA, pp. 163–197.
- Matthews, A., Dickman, C.R., Major, R.E., 1992. The influence of fragment size and edge on nest predation in urban bushland. *Ecography* 22, 349–356.
- Møller, A.P., 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. *Oikos* 56, 240–246.
- Ortega, C.P., Ortega, J.C., Rapp, C.A., Vorisek, S., Backensto, S.A., Palmer, D.W., 1997. Effect of research activity on the success of American robin nests. *Journal of Wildlife Management* 61, 948–952.
- Ortega, C.P., Ortega, J.C., Rapp, C.A., Backensto, S.A., 1997. Validating the use of artificial nests in predation experiments. *Journal of Wildlife Management* 62, 925–932.
- Paton, P.W.C., 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8, 17–26.
- Reitsma, L.R., Holmes, R.T., Sherry, T.W., 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57, 375–380.
- Ricklefs, R.E., 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9.
- Robinson, S.K., Thompson III, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267, 1987–1990.
- Rudnický, T.C., Hunter Jr., M.L., 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57, 358–364.
- Skutch, A.F., 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. *Ornithological Monographs* 36, 575–603.
- Slater, P., Slater, P., Slater, R., 1997. *The Slater Field Guide to Australian Birds*. Lansdowne, Australia.
- Sloan, S.S., Holmes, R.T., Sherry, T.W., 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwood forest. *Journal of Wildlife Management* 62, 529–539.
- StatSoft Inc., 1995. *Statistica for Windows*. StatSoft Inc., Tulsa, Oklahoma, USA.
- Tellería, J.L., Santos, T., 1992. Spatiotemporal patterns of egg predation in forest islands: an experimental approach. *Biological Conservation* 62, 29–33.
- Temple, S.A., Cary, J.R., 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2, 340–347.
- Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66, 1211–1214.
- Willebrand, T., Marcström, V., 1988. On the danger of using dummy nests to study predation. *Auk* 105, 378–379.
- Wilson, G.A., Brittingham, M.C., Goodrich, L.J., 1998. How well do artificial nests estimate success of real nests? *Condor* 100, 357–364.
- Yahner, R.H., Mahan, C.G., 1996. Depredation of artificial ground nests in a managed, forested landscape. *Conservation Biology* 10, 285–288.
- Yahner, R.H., Morrell, T.E., Rachael, J.S., 1989. Effects of edge contrast on depredation of artificial avian nests. *Journal of Wildlife Management* 53, 1135–1138.
- Yahner, R.H., Voytko, R.A., 1989. Effects of nest-site selection on depredation of artificial nests. *Journal of Wildlife Management* 53, 21–25.
- Zanette, L., 1997. Predation of an eastern yellow robin nest by a small bird, the brown-headed honeyeater. *The Australian Birdwatcher: a Journal of Field Ornithology* 17, 158–159.
- Zanette, L., Jenkins, B., 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. *Auk* 117, 445–454.
- Zanette, L., Doyle, P., Trémont, S.M., 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81, 1654–1666.