

## PREDATION OF NATURAL AND ARTIFICIAL NESTS IN A SOUTHERN PINE FOREST

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**ABSTRACT.**—We compared predation of artificial open-cup nests baited with Japanese Quail (*Coturnix coturnix*) eggs with predation of natural open-cup nests during 1997 and 1998 in a Louisiana pine forest to assess the assumption that predation of artificial nests is an index to that of natural nests. Cameras were placed at randomly selected natural and artificial nests in shrubs to document predators. Predation at artificial-nest plots was positively correlated with predation at adjacent natural-nest plots overall, although inconsistently by year. Artificial nests were almost exclusively depredated by corvids, but quail eggs were too large to be broken by small-mouthed mammalian predators. American Crows (*Corvus brachyrhynchos*) appeared to be important predators of natural nests. Predation of natural nests was independent of predation at other nests, but predation of artificial nests by crows was spatially and temporally clumped. Crows may have learned the location of artificial-nest plots, and predation of artificial nests increased significantly between years, contrary to predation of natural nests. Predation of artificial nests did not exhibit seasonal variation like that of natural nests. Overall, predation of artificial shrub nests did not accurately mimic that of natural shrub nests. Changes in procedures for artificial-nest studies that reduce spatially and temporally clumped predation and prevent the exclusion of small-mouthed predators could increase the suitability of such studies as a model for predation at natural nests. However, the difference in labor effort between studies of natural nests versus artificial nests that incorporate the changes we recommend likely would disappear, which would reduce the attractiveness of artificial-nest studies as an experimental model. Received 13 September 1999, accepted 11 January 2000.

PREDATION is the leading cause of nesting mortality in most passerines (Ricklefs 1969, Martin 1995) and undoubtedly is a contributing factor to recent declines in abundance of many breeding songbirds in temperate North America (Robbins et al. 1989, Askins et al. 1990). As a result, many researchers have focused on examining nest predation. Artificial-nest experiments often are used to test hypotheses concerning nest predation because the number, appearance, placement, and contents of artificial nests can be controlled and manipulated. Moreover, the effort and cost to gather data are much lower for artificial nests than for natural nests.

Artificial nests typically do not have rates of predation equal to natural nests, but researchers assume that predation rates of artificial nests provide an index of those of natural nests (Major and Kendal 1996). Lind (1997) tested this assumption and found that predation rates

of open-cup songbird nests were not correlated with those of artificial nests in adjacent plots in a Louisiana hardwood forest. However, under certain circumstances artificial nests may be equivalent to natural nests for some predators, and additional comparisons of predation at natural versus artificial nests are needed.

The suite of nest predators can vary between natural and artificial nests. For example, some studies have found that birds are the main predators of artificial nests and mammals of natural nests (Willebrand and Marcström 1988, MacIvor et al. 1990). How this difference in predators affects predation rates of natural and artificial nests is unknown. In this study, we compare predation at paired natural and artificial nest plots to determine if predation of artificial nests provides an index to predation of natural nests and to examine temporal patterns of predation between nest types. We also compare predators of natural and artificial open-cup nests.

### STUDY AREA AND METHODS

*Study area.*—This study was conducted on the East Reservation of Barksdale Air Force Base in Bossier

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City, Louisiana, in 1997 and 1998. This 3,000-ha forest is highly fragmented by clearcuts, natural gas wells, pipeline corridors, and dirt roads. Major canopy trees are shortleaf pine (*Pinus echinata*) and loblolly pine (*Pinus taeda*), with scattered sweetgum (*Liquidambar styraciflua*) and oaks (*Quercus* spp.). Common understory trees and shrubs include sweetgum, blackjack oak (*Quercus marilandica*), winged elm (*Ulmus alata*), flowering dogwood (*Cornus florida*), dewberry (*Rubus* spp.), and waxmyrtle (*Myrica cerifera*). Periodic burning of the pine forest created a dense understory with little midstory vegetation.

**Nest plots.**—We searched in 12 plots (12 ha each) for songbird nests within older (trees >50 years old) upland pine habitats. Plots were adjacent to four edge types (clearcut, pipeline, road, and natural gas well) as part of an ongoing study of edge effects on songbird productivity. Each plot was marked with grid points spaced at 25-m intervals. The location of nests was marked with flagging at least 5 m from the nest, and the grid location was noted. Nests typically were monitored every three days (Martin and Guepel 1993). A nest was considered depredated if its contents were removed before the young were capable of leaving the nest.

We established an artificial-nest plot adjacent to each natural-nest plot; paired plots were similar in habitat and edge characteristics. Plots were paired to increase the likelihood that nests on each pair were exposed to the same predators. Artificial-nest plots were 50 to 400 m from their respective natural-nest plots, except for one that was 2 km away. Paired plots were closer to each other than to plots of other pairs in all but two cases (limited patches of adequate size were available to incorporate natural nest plots and maintain similar edge characteristics among pairs).

**Artificial nests.**—We used techniques common to artificial-nest experiments so results would be comparable to past experiments. We placed artificial nests in dense grid patterns atypical of natural nest locations despite possible density-dependent effects (Sugden and Beyersbergen 1986, Keyser et al. 1998, Ortega et al. 1998, Sloan et al. 1998; but see O'Reilly and Hannon 1989, Reitsma 1992). We baited nests with two Japanese Quail (*Coturnix coturnix*) eggs, even though small-mouthed predators may not be able to puncture these eggs (Roper 1992, Haskell 1995a). Twenty artificial nests were placed within each plot at 25-m intervals along two or three parallel transect lines set 50 m apart. Nests were randomly placed between 0.1 and 2.0 m above ground and secured to forks or the main stem of vegetation by wire. We constructed artificial nests from chicken wire and lined them with dried vegetation from the study site to make them resemble natural open-cup nests. Nests were checked every three days (same as natural nests) to determine fates and were removed after 12 days. Nests with at least one egg missing or damaged were classified as depredated. Two trials were

conducted each breeding season. Plots were randomly assigned to one of three consecutive 12-day sampling periods in each trial period.

**Predator identification.**—To document predators, Kodak DC-40 digital or Polaroid 3000AF film cameras were placed 1.5 m from selected natural and artificial nests, respectively. Cameras had automatic flashes and recorded the day, hour, and minute when pictures were taken. We randomly monitored one out of every three natural "shrub" nests (0.1 to 2 m above the ground) with a camera. Film cameras were placed at seven to nine randomly chosen artificial nests on each plot during each trial.

In 1997, OPTEK FX35S passive-infrared-motion/heat detectors powered with rechargeable 12-volt batteries were used to trigger cameras. Motion detectors were placed about 50 cm from nests to ensure that the smallest potential predators could be detected. Because many images of attending adult birds were recorded at natural nests, and each camera could store only 99 images, digital cameras were visited every one to two days to clear the memory and check the battery. Cameras monitoring artificial nests were checked for battery or film replacement during regular nest checks because they recorded images only when a nest was disturbed.

We classified individual animals observed at artificial nests into two categories: "predators" and "visitors." Predators were photographed in direct contact with an egg or while disturbing a nest that was later depredated. In several instances, multiple species and/or observations were made at one nest and the actual predator could not be determined; these were classified as visitors.

We changed the triggering mechanism in 1998 because we only captured predation at 14% of 35 monitored artificial nests that were depredated and because of problems created by multiple observations at nests. When eggs were removed from the nest in 1998, a Cherry E21-85HX microswitch attached to an egg in the nest triggered the camera. Nylon fishing line was glued to either a host egg or a quail egg, threaded through the bottom of the nest, and tied to the lever of the microswitch. These cameras recorded 50% ( $n = 138$ ) of the known predation events.

**Data analysis.**—We performed paired *t*-tests of predation at camera-monitored and camera-free nests to determine camera effects within plots by trial. Plots were considered the experimental unit rather than nests unless otherwise stated. We could not test for camera effects at natural-nest plots because of low sample sizes. Therefore, we pooled nests across plots and years and used CONTRAST (Hines and Sauer 1989) to compare daily predation rates at camera-monitored versus camera-free natural shrub nests. Daily predation rates for natural-nest plots were calculated using the Mayfield method (Mayfield 1961, 1975), with variances calculated according to Johnson (1979). Only data from nests with known out-

TABLE 1. Predation rates ( $\bar{x} \pm SE$ ) at camera-free and camera-monitored artificial nests within plots by trial and year.

Trial	Camera-free nests	Camera nests	Paired <i>t</i>	df	<i>P</i>
<b>1997</b>					
1	29.4 ± 8.5	20.0 ± 9.1	2.2	10	0.05
2	30.6 ± 12.5	28.1 ± 13.8	0.6	7	0.55
<b>1998</b>					
1	72.9 ± 9.2	70.0 ± 11.9	0.5	11	0.63
2	78.5 ± 7.7	79.2 ± 9.0	-0.2	11	0.87

comes were used to calculate daily predation rates, with nests being the experimental units.

To test for seasonal variation in predation of natural nests, we divided the breeding season into "early" and "late." Late nests were initiated after the beginning of trial 2 of the artificial-nest experiment each year (11 June 1997 and 30 May 1998). We used CONTRAST to compare daily predation rates for early and late shrub nests. Again, we pooled nests across plots because of low sample sizes. To test for seasonal variation in predation of artificial nests, we compared differences in predation at artificial nests on each plot between trials. We excluded data from four plots that were burned after the 1997 breeding season.

For testing continuous variables, we used group and paired *t*-tests after checking data for normality. For comparing categorical data, we used chi-square contingency and goodness-of-fit tests. An  $\alpha$  less than 0.05 was considered significant; means are presented  $\pm 1$  SE.

We used Pearson correlations to test for an association between predation at natural-nest plots and artificial-nest plots. We controlled for differences in exposure days between natural and artificial nests by calculating the proportion of natural open-cup nests depredated during 12 exposure days (predation rate) of natural-nest plots using the following equation:

$$1 - (1 - \text{daily predation rate})^{12}. \quad (1)$$

The predation rate for each artificial-nest plot was simply the average proportion of nests depredated on the plot during both trials. Predation rates were arcsine transformed to meet the assumption of normality. We tested years separately and combined. We used principal axes analysis (Sokal and Rohlf 1995: 586-595) to characterize the trend of the association between natural and artificial nest predation as a line. Simple linear regression, which minimizes sum of squares deviations parallel to the *Y* axis (only with respect to *Y*, not *X*), is not appropriate because both variables are random and measured with error. Principal axes analysis minimizes the sum of squares deviations perpendicular to the principal axes of the confidence ellipse about the bivariate mean (with re-

spect to both  $\bar{Y}_1$  and  $\bar{Y}_2$ ). We also performed an *a posteriori* correlation test between natural and artificial nest predation where we included predation by small-mouthed predators based on scratch marks on eggs or mouse droppings in nests and excluded cases of "trap-lining" by American Crows (*Corvus brachyrhynchos*) when 10 or more artificial nests were destroyed on a plot during one check period.

## RESULTS

**Nest predation.**—In 1997, 82 of 278 (29%) nests were depredated on the 12 natural-nest plots, and in 1998, 87 of 205 (42%) nests were depredated. Of the 483 open-cup nests found, 218 occurred in the shrub layer between 0.1 and 2.0 m above ground and were used for comparisons with artificial nests. The most frequently found shrub nests were of Northern Cardinals (*Cardinalis cardinalis*; 40%), Indigo Buntings (*Passerina cyanea*; 24%), and White-eyed Vireos (*Vireo griseus*; 15%). We determined the fates of 378 artificial nests in 1997 and 478 in 1998; 103 (27%) and 360 (75%) of the artificial nests were depredated each year, respectively.

**Camera effects.**—Daily predation rate for 42 camera-monitored natural shrub nests ( $0.013 \pm 0.006$ ) was significantly lower ( $\chi^2 = 11.7$ , *df* = 1,  $P < 0.01$ ) than that for 176 camera-free nests ( $0.039 \pm 0.004$ ). Camera-monitored shrub nests were abandoned (58%,  $n = 19$ ) more frequently ( $\chi^2 = 69.2$ , *df* = 2,  $P < 0.01$ ) than camera-free shrub nests (10%;  $n = 93$ ). Because of the effects of cameras, we did not include data from camera-monitored natural shrub nests in calculations of predation rates. For artificial nests, cameras did not significantly affect predation rates in all but the first trial of 1997, where camera-monitored nest failure was lower (Table 1). These data (excluding the first trial of 1997)

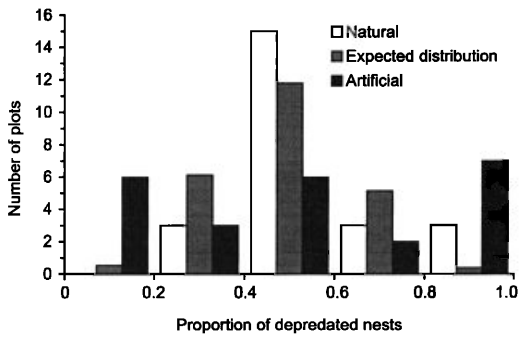


FIG. 1. Frequency distribution of predation rates for natural-nest and artificial-nest plots versus expected binomial distribution for combined years.

were included in the analysis of predation rates.

*Independence of individual nests.*—Overall mean predation rates of natural-nest ( $0.449 \pm 0.027$ ) and artificial-nest plots ( $0.522 \pm 0.072$ ) were similar ( $t = -1.3$ ,  $df = 23$ ,  $P = 0.22$ ), but the frequency distributions of predation rates differed between natural and artificial nests. Predation rates in natural-nest plots did not differ from a binomial distribution ( $\chi^2 = 4.8$ ,  $df = 4$ ,  $P = 0.31$ ; Fig. 1); thus, fates of individual nests were considered independent. In artificial-nest plots, however, predation rates differed significantly from that of a binomial distribution with an excess of observations at the tails of the distribution ( $\chi^2 = 22.2$ ,  $df = 4$ ,  $P < 0.01$ ). Thus, fates of individual artificial nests within plots were not independent.

Predation was temporally clumped for artificial-nest plots with the highest predation. On five occasions during 1998, all 20 nests on artificial-nest plots were depredated before the first check. Crows photographed at these nests apparently had "trap-lined" the nests by destroying several in a few minutes to several hours. The presence of crows at artificial-nest plots was associated ( $\chi^2 = 4.0$ ,  $df = 1$ ,  $P = 0.05$ ) with trap-lining. Trap-lining occurred in one sample on an artificial-nest plot in 1997 and in 11 samples among six artificial-nest plots in 1998. Once trap-lining occurred on an artificial-nest plot, it continued on all subsequent trials on that plot.

*Correlation of predation rates.*—The correlation of predation rates between natural-nest and artificial-nest plot pairs was significant ( $R^2 = 0.45$ ,  $n = 24$ ,  $P < 0.01$ ; Fig. 2) for the combined

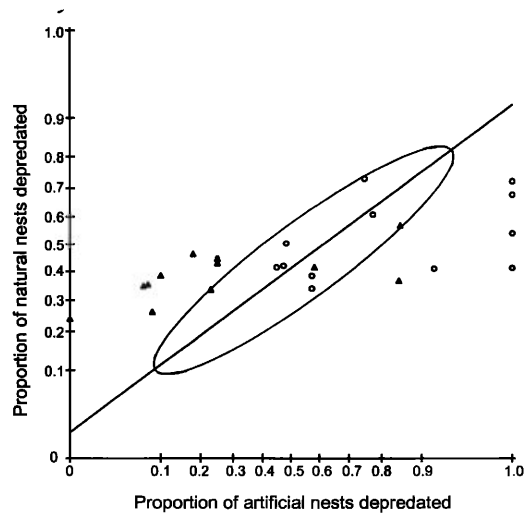


FIG. 2. Nest-predation rates on natural-nest plots and adjacent artificial-nest plots in 1997 (closed triangles) and 1998 (open circles). The slope of the principal axis is 0.77 with the 95% confidence ellipse of the bivariate mean presented. Data are plotted on an arithmetic probability scale.

years and for 1997 alone ( $R^2 = 0.42$ ,  $n = 12$ ,  $P = 0.02$ ), but not for 1998 alone ( $R^2 = 0.21$ ,  $n = 12$ ,  $P = 0.13$ ). The principal axis of the relationship between predation rates for the combined years had a slope of 0.77 (Fig. 2). The 95% confidence interval for this slope ranged from 0.64 to 0.91. The slope of the major axis for 1997 was 1.07.

The *a posteriori* correlation in which trap-lined nest plots were removed and small-mouthed mammal visitation was considered predation was significant for the combined years ( $R^2 = 0.58$ ,  $n = 18$ ,  $P < 0.01$ ) and for 1997 ( $R^2 = 0.56$ ,  $n = 11$ ,  $P = 0.01$ ) and approached significance for 1998 ( $R^2 = 0.49$ ,  $n = 7$ ,  $P = 0.08$ ). The principal axis of the relationship between predation rates for combined years had a slope of 1.00 (Fig. 3). The 95% confidence interval for this slope ranged from 0.89 to 1.14. The slope of the major axis for 1997 was 1.08 and for 1998 was 0.93.

*Temporal differences of predation rates.*—Daily predation rate of natural nests was lower early in the breeding season ( $0.019 \pm 0.003$ ) than late ( $0.031 \pm 0.005$ ;  $\chi^2 = 4.6$ ,  $df = 1$ ,  $P = 0.03$ ). No significant seasonal differences in predation rates occurred between early ( $0.540 \pm 0.090$ ) and late ( $0.617 \pm 0.089$ ) nests on artificial-nest plots ( $t = -0.9$ ,  $df = 18$ ,  $P = 0.38$ ).

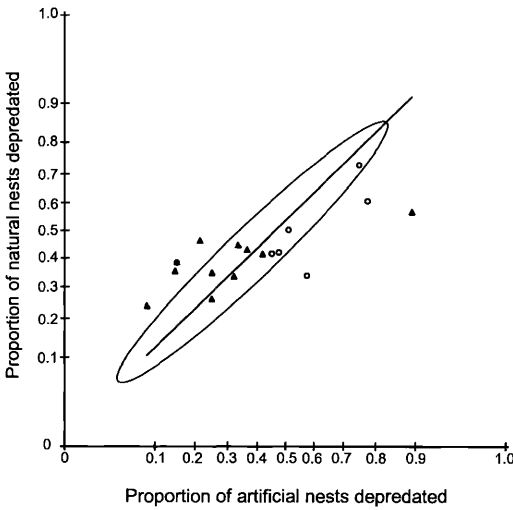


FIG 3. *A posteriori* adjusted nest-predation rates on natural-nest plots and adjacent artificial-nest plots in 1997 (closed triangles) and 1998 (open circles). The slope of the principal axis is 1.00 with the 95% confidence ellipse of the bivariate mean presented. Data are plotted on an arithmetic probability scale.

Mean predation rates on artificial-nest plots were much higher in 1998 ( $0.751 \pm 0.066$ ) than in 1997 ( $0.293 \pm 0.086$ ;  $t = -5.4$ ,  $df = 11$ ,  $P < 0.01$ ), whereas predation rates on natural-nest plots were more similar between years (1997,  $0.401 \pm 0.034$ ; 1998,  $0.520 \pm 0.055$ ;  $t = -2.0$ ,  $df = 7$ ,  $P = 0.09$ ). In addition, the mean relative difference in nest predation between years on artificial-nest plots was marginally higher than that for natural-nest plots ( $t = -2.0$ ,  $df = 7$ ,  $P = 0.09$ ). When we adjusted predation rates of artificial-nest plots to account for small-mouthed predators and the exclusion of trap-lining by crows, the mean relative difference in predation of artificial nests between years was

not significantly different than that of natural nests ( $t = -1.5$ ,  $df = 5$ ,  $P = 0.20$ ).

**Predators.**—Cameras at 327 artificial nests recorded 74 predation and 19 visitation events (Table 2). In addition, we documented 35 visitations by mice (excrement and/or scratch marks on eggs) and 5 nest infestations (4 by fire ants, 1 by an unidentified insect) during nest visits. Scratch marks on damaged eggs, egg fragments, and excrement in the nest identified small-mouthed mammals as predators at eight additional nests.

Crows were responsible for 61%, Blue Jays (*Cyanocitta cristata*) 29%, and small-mouthed mammals 10% of predation events at artificial nests for both years combined ( $n = 82$ ). The only small-mouthed mammal identified from photographs was the golden mouse (*Ochrotomys nuttallii*), but other potential small-mouthed mammals probably were present. No scratch marks or droppings were found at two of the seven artificial nests at which mice were photographed. Thus, small-mouthed mammals did not always leave marks on eggs that they attempted to consume. Other visitors observed at artificial nests included Carolina Wren (*Thryothorus ludovicianus*), Carolina Chickadee (*Poecile carolinensis*), Brown-headed Cowbird (*Molothrus ater*), Pine Warbler (*Dendroica pinus*), and fox squirrel (*Sciurus niger*).

Of the 42 natural shrub nests monitored by cameras, no observations of predation were recorded. Field assistants observed predators at natural nests in a few instances, including black rat snake (*Elaphe obsoleta*), buttermilk racer (*Coluber constrictor*), Blue Jay, and American Crow. The occurrence of crow predation at artificial-nest plots was associated with high relative predation at their adjacent natural-nest plots (Table 3). The occurrence of Blue Jay predation at artificial-nest plots was not associated

TABLE 2. Frequency (% in parentheses) of animals depredating or visiting artificial nests by year based on camera or nest evidence.

Species	Predation		Visitation	
	1997	1998	1997	1998
American Crow	5 (71)	45 (60)	4 (8)	
Blue Jay		24 (32)	1 (2)	
Carolina Wren			3 (6)	
Small-mouthed mammal	2 (29)	6 (8)	36 (70)	4 (67)
Fire ant			4 (8)	
Other			3 (6)	2 (33)

TABLE 3. Association between nest-predation rates on natural-nest plots and presence of predators (crows and jays) on adjacent artificial-nest plots. Values are number of nest plots.

Predator at artificial-nest plot	Relative predation rate on natural-nest plot		<i>P</i> <sup>a</sup>
	Low	High	
<b>American Crow</b>			
Yes	1	6	0.015
No	5	0	
<b>Blue Jay</b>			
Yes	5	4	1.000
No	1	2	

<sup>a</sup> Fisher's exact test.

with relative depredation at adjacent natural-nest plots.

#### DISCUSSION

Mean predation rates were similar at artificial-nest and natural-nest plots, and predation at artificial-nest plots was positively correlated with that at adjacent natural-nest plots. Only 45% of the variation in predation rates between nest types was explained by the correlation, but certainly some of the variance can be attributed to measurement error and placement of plot pairs. We did not find all of the natural nests within plots, and a combined four-week period of evaluating predation of individual artificial-nest plots may not fully represent predation that would have occurred during the entire breeding season within these plots. Also, two plot pairs were closer to plots of other pairs, and one artificial-nest plot was located 2 km from the paired natural-nest plot. Thus, it is difficult to evaluate the strength of this index based on the amount of variation it explains. We note that the correlation was significant only in 1997 when years were tested separately, indicating a lack of robustness between years. In only one study, for ducks, was nesting success at artificial nests significantly linearly related to that at natural nests (Butler and Rotella 1998). As in our study, the relationship differed between years.

Predation of artificial nests, in general, is a poor index to that of natural nests across years (Willebrand and Marcström 1988, Guyn and Clark 1997, Butler and Rotella 1998). Consistent with this, the magnitude of the relative increase of predation between years for artificial nests was three times that of natural nests. This

was due to the increased trap-lining activity of crows in 1998, because the relative abundance of the major predators, crows and jays, did not increase between years based on 5-min point counts at natural-nest plots (M. Baker pers. comm.). Moreover, artificial nests failed to mimic within-season variation of predation of natural nests.

Crows were the main predators of artificial nests, consistent with findings of others in largely fragmented landscapes (Yahner and Wright 1985, Angelstam 1986, Yahner and Voytko 1989, Nour et al. 1993). Crows also were important predators of natural nests, because their presence at artificial-nest plots was associated with relatively high predation on adjacent natural-nest plots. Crows, however, appeared to depredate artificial nests differently than natural nests. Trap-lining of forest songbird nests has not been reported, nor was it evident in our study, but during the second trial in 1997 of the artificial-nest experiment, crows began trap-lining artificial nests. Crows appeared to learn the locations of artificial-nest plots because once nest trap-lining occurred, all subsequent samplings of that plot had trap-lined nests. Trap-lining of artificial open-cup nests has been reported (O'Reilly and Hannon 1988, Keyser et al. 1998, Wilson et al. 1998) and attributed to predators such as fishers (*Martes pennanti*; Sloan et al. 1998), Hooded Crows (*Corvus corone*; Götmark et al. 1990), black bears (*Ursus americanus*) and raccoons (*Procyon lotor*; Reitsma et al. 1990), and Blue Jays (Yahner and Wright 1985).

Artificial nests typically are more evenly and densely placed, less protected, and more visible than natural nests. These conditions may fa-

cilitate, in crows and other visual predators, quick development of a search image for artificial nests because crows increase their time hunting in areas following successful foraging, especially where nest densities are high (Tinbergen et al. 1967, Sugden and Beyersbergen 1986). Cameras may have acted as a marker to the presence of artificial nests, which also may aid crows to develop a search image (Yahner and Wright 1985). However, cameras did not cue predators to the presence of individual artificial nests because camera-monitored nests experienced similar predation to camera-free nests. In fact, cameras initially deterred predators from artificial nests (during the first trial), and they also deterred predators from natural nests overall because camera-monitored nests experienced lower predation rates than camera-free nests.

We also found differences in the types of predators at artificial and natural nests. Snakes are an important predator of shrub-nesting passerines in old-field habitat of Missouri (Thompson et al. 1999) and were predators of natural nests in our study. Snakes, however, have never been observed depredating artificial nests, and captive snakes do not eat quail eggs (Marini and Melo 1998). Most small-mouthed predators (mice) were excluded from predation of artificial nests because they rarely destroyed the relatively large quail eggs. Mice were frequent visitors to artificial nests and would have been important predators had they been able to penetrate the shells of quail eggs. Exclusion of predation by small-mouthed mammals at artificial nests baited with quail eggs is well known (Roper 1992; Haskell 1995a, b), but the importance of mice as predators of natural nests is relatively unknown (but see Maxson and Oring 1978, Guillory 1987).

Correlations between predation rates alone are not adequate support for using predation of artificial nests as an index to that of natural nests because the correlation we found belied the most critical differences in how natural and artificial nests were depredated. Artificial nests failed to mimic variation within and between years in predation of natural nests, predators differed between nest types, and crows trap-lined artificial nests but not natural nests. These differences, coupled with the lack of robustness of the overall correlation, lead us to conclude that predation of artificial shrub nests

does not accurately mimic that of natural shrub nests in a highly fragmented pine forest of Louisiana.

After discovering trap-lining and predator differences between natural and artificial nests, we attempted to determine how they influenced our results by reevaluating the relationship between predation of artificial and natural nests. Admittedly, our attempt to quantify trap-lining and to eliminate it was somewhat arbitrary, yet it was conservatively based on the data. We considered the depredation of 10 or more artificial nests (50%) on a plot during one check period to constitute trap-lining because most nest losses were clumped at 5 or fewer nests or 10 or more nests. This split in the data quantified what we considered trap-lining. We could not fully account for predation by small-mouthed mammals because of the paucity of evidence of visitation by them. Regardless, the *a posteriori* correlation between predation rates on natural and artificial nest plots was more robust and characterized by a one-to-one relationship for the combined years. The correlation in 1998 had a lower *P*-value than the *a priori* analysis, although it was not quite significant. In addition, the magnitude of between-year variation for natural and artificial nests was similar, yet within-season variation differed between nest types. Thus, if the differences of trap-lining and predator types of natural versus artificial nests can be reduced (indicating that predators perceive artificial and natural nests similarly), artificial nests may serve as better surrogates of natural nests for examining predation. Researchers should bear in mind, however, that accumulating evidence based on different methods and in various systems suggests that predation of artificial nests does not mimic that of natural nests.

Trap-lining may be eliminated or greatly reduced by changes in experimental design. Placing artificial nests in diverse locations, at varying times, and in lower densities, rather than flooding the habitat with a dense grid of identically placed nests, will create a mosaic of "active" nests. This placement will better resemble the natural occurrence of forest songbird nests and may eliminate the problem of trap-lining. If researchers continue to place nests in a high density, they should only sample plots once and use different plots for replicates to avoid having predators learn the locations of nest

plots. These changes, however, would eliminate two of the most attractive features of artificial-nest experiments: simplicity of design and control. Moreover, artificial-nest experiments may become just as labor intensive and expensive as the monitoring of natural nests, thus reducing the advantages of artificial-nest studies. Even with these changes, fundamental problems may remain with the use of artificial nests (i.e. lack of parental activity, begging noise, and natural scent; King et al. 1999). These problems must be addressed to improve the usefulness of experiments based on artificial nests.

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#### LITERATURE CITED

- ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- ASKINS, R. A., J. F. LYNCH, AND R. S. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7: 1-57.
- BUTLER, M. A., AND J. J. ROTELLA. 1998. Validity of using artificial nests to assess duck-nest success. *Journal of Wildlife Management* 62:163-171.
- GÖTMARK, F., R. NEERGAARD, AND M. ÅHLUND. 1990. Predation of artificial and real Arctic Loon nests in Sweden. *Journal of Wildlife Management* 54: 429-432.
- GUILLORY, H. D. 1987. Cavity competition and suspected predation on Prothonotary Warblers by *Peromyscus* spp. *Journal of Field Ornithology* 58: 425-427.
- GUYN, K. L., AND R. G. CLARK. 1997. Survival characteristics of natural and artificial duck nests. *Journal of Field Ornithology* 68:33-41.
- HASKELL, D. G. 1995a. Forest fragmentation and nest predation: Are experiments with Japanese Quail eggs misleading? *Auk* 112:767-770.
- HASKELL, D. G. 1995b. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* 9:1316-1318.
- HINES, J. E., AND J. R. SAUER. 1989. Program CON-TRAST: A general program for the analysis of several survival or recovery rate estimates. United States Fish and Wildlife Service Resource Publication No. 24.
- JOHNSON, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96: 651-661.
- KEYSER, A. J., G. E. HILL, AND E. C. SOEHREN. 1998. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. *Conservation Biology* 12:986-994.
- KING, D. I., R. M. DEGRAAF, C. R. GRIFFIN, AND T. J. MAIER. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? *Journal of Field Ornithology* 70: 257-262.
- LIND, J. W. 1997. A comparison of nest success between forest edge and interior habitats: Data from natural and artificial songbird nests. M.S. thesis, Louisiana State University, Baton Rouge.
- MACIVOR, L. H., S. M. MELVIN, AND C. R. GRIFFIN. 1990. Effects of research activity on Piping Plover nest predation. *Journal of Wildlife Management* 54:443-447.
- MAJOR, R. E., AND C. E. KENDAL. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. *Ibis* 138:298-307.
- MARINI, M. Â., AND C. MELO. 1998. Predators of quail eggs, and the evidence of the remains: Implications for nest predation studies. *Condor* 100:395-399.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.
- MARTIN, T. E., AND G. R. GUEPEL. 1993. Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507-519.
- MAXSON, S. J., AND L. W. ORING. 1978. Mice as a source of egg loss among ground-nesting birds. *Auk* 95:582-532.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- MAYFIELD, H. F. 1975. Suggestions for calculation of nest success. *Wilson Bulletin* 87:456-466.
- NOUR, N., E. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: Different trends in bird and mammal predators. *Ecography* 16:111-116.
- O'REILLY, P., AND S. J. HANNON. 1989. Predation of simulated Willow Ptarmigan nests: The influence of density and cover on spatial and temporal patterns of predation. *Canadian Journal of Zoology* 67:1263-1267.
- ORTEGA, C. P., J. C. ORTEGA, C. A. RAPP, AND S. A. BACKENSTO. 1998. Validating the use of artificial



- nests in predation experiments. *Journal of Wildlife Management* 62:925-932.
- REITSMA, L. R. 1992. Is nest predation density dependent? A test using artificial nests. *Canadian Journal of Zoology* 70:2498-2500.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 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* 9:1-48.
- ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences USA* 86:7658-7662.
- ROPER, J. J. 1992. Nest predation experiments with quail eggs: Too much to swallow? *Oikos* 65:528-530.
- SLOAN, S. S., R. T. HOLMES, AND T. W. SHERRY. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* 62:529-539.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman, San Francisco.
- SUGDEN, L. G., AND G. W. BEYERSBERGEN. 1986. Effects of density and concealment on American Crow predation of simulated duck nests. *Journal of Wildlife Management* 50:9-14.
- THOMPSON, F. R. III, W. D. DIJAK, AND D. E. BURHANS. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259-264.
- TINBERGEN, N., M. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28:307-321.
- WILLEBRAND, T., AND V. MARCSTRÖM. 1988. On the danger of using dummy nests to study predation. *Auk* 105:378-379.
- WILSON, G. R., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1998. How well do artificial nests estimate success of real nests? *Condor* 100:357-364.
- YAHNER, R. H., AND R. A. VOYTKO. 1989. Effects of nest-site selection on depredation of artificial nests. *Journal of Wildlife Management* 53:21-25.
- YAHNER, R. H., AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: Effects of edge and plot age. *Journal of Wildlife Management* 49:508-513.

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