ARTIFICIAL NEST EXPERIMENTS: EFFECTS OF NEST APPEARANCE AND TYPE OF PREDATOR[1]

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Nest predation is a primary cause of nesting mortality for many bird species (Skutch 1949, 1966; Nice 1957; Ricklefs 1969; Nilsson 1984). Food limitation and competition also can affect nesting success (see reviews in Martin 1986, 1987). However, the primary role of nest predation in nesting mortality suggests that it can be a strong agent of selection on bird species and assemblages; when nest predation differs among species, habitats, and areas, it can influence life history traits, habitat use, and population and community patterns (Duebbert and Kantrud 1974; Slagsvold 1982; Martin, unpubl.).

Intensity of nest predation differs among groups of birds based on the nesting substrates and heights of their nests (Ricklefs 1969, Nilsson 1984), between island and mainland areas (Loiselle and Hoppes 1983, Savidge 1987), and among habitat islands of different sizes (Wilcove 1985). One means of documenting such differences in nest predation is through controlled experiments using artificial nests. Two recent studies (Loiselle and Hoppes 1983, Wilcove 1985) used artificial wicker nests to examine differences in predation rates for different nest types, habitats, and areas. Both studies used wicker nests with leaves or straw lining the inside of the nest and without modification of the outside of the nest (e.g., Loiselle and Hoppes 1983, Wilcove 1985). Wilcove (1985) noted that these nests were more conspicuous than real nests. Consequently, both he and Loiselle and Hoppes (1983) felt that artificial nests did not measure the actual rate of predation that birds experience, but they assumed that any biases were consistent among sites and nest types. However, this crucial assumption requires testing before further experiments are conducted. In this paper, I report results of experiments that test effects of nest appearance and placement on probability of nest predation.

STUDY AREA AND METHODS

Study sites were located in high elevation (2,300 m) forest on the Mogollon Rim in central Arizona. The rim is characterized by long canyons with numerous small drainages along their sides. These drainages have a canopy comprised of ponderosa pine (Pinus ponder-

osa), white fir (Abies concolor), douglas-fir (Pseudotsuga Menziesii), white pine (Pinus strobiformis), gambel oak (Quercus gambellii), and quaking aspen (Populus tremuloides). The understory is dominated by big tooth maple (Acer grandidentatum) with New Mexican locust (Robinia neomexicana) and young firs also common. These drainages are surrounded by continuous forest that is dominated by ponderosa pine.

Many potential nest predators are present on the study sites. Red squirrels (Tamiasciurus hudsonicus) are extremely abundant. Least chipmunks (Eutamias minimus) are also abundant and commonly seen in small white firs, the nest sites of three bird species (see below). Golden-mantled ground squirrels (Citellus lateralis) and deer mice (Peromyscus maniculatus) are common and potential ground nest predators. I have seen long-tailed weasels (Mustela frenata) on several occasions over 4 years, but their relative abundance is unknown. Other larger mammals present on the sites that are potential nest predators include coyotes (Canis latrans), striped skunks (Mephitis mephitis), bobcats (Lynx rufus), and black bears (Ursus americanus). Snakes on the sites include western garter snakes (Thamnophis elegans) and bullsnakes (Pituophis melanoleucus). Avian predators include Steller's Jays (Cyanocitta stelleri).

Two drainages (plots 1 and 2), each about 7 ha in area and 5 km apart, were used as spatial replicates. Experiment 1 was conducted on plot 1 using 30 nests from 22 May to 4 June 1986. Experiment 2 was conducted on both plots using 60 nests per plot from 10 to 25 June 1986. Plot 1 was used in both experiments to provide a temporal replicate to examine whether patterns of nest predation are consistent through time. Three nest types were used in experiment 1. One nest type was an artificial open-cup, wicker nest modified only by lining the inside with leaves (artificial nest hereafter). The second nest type was an artificial wicker nest that was lined on the inside and outside with various mosses (moss nest hereafter) to resemble appearance of natural Hermit Thrush (Catharus guttatus) and MacGillivray's Warbler (Oporornis tolmiei) nests. The third nest type was real nests of Hermit Thrushes (primarily) and MacGillivray's Warblers (real nests hereafter) that were collected in 1985 and stored over winter. All three nest types were placed in small white firs (0.5 to 3 m tall) at 0.5 to 2 m off the ground (hereafter referred to as off-ground nests) because these are the sites used most commonly by Hermit Thrushes, MacGillivray's Warblers, and Green-tailed Towhees, Pipilo chlorurus (Martin, unpubl. data). The three nest types were alternated systematically and placed at ap-
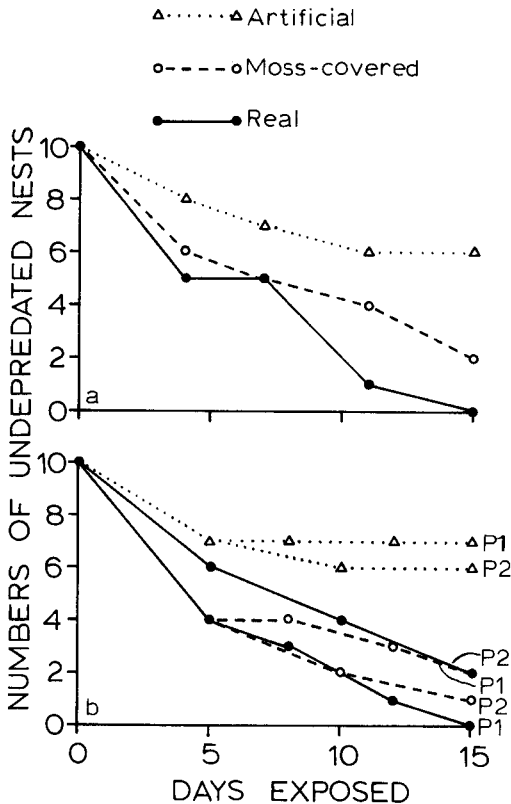
FIGURE 1. Numbers of undepredated nests relative to numbers of days exposed for off-ground nests. (a) Experiment 1 on plot 1. The loglinear slopes ± standard errors for the three types of nests are: real (-3.55 ± 0.36), artificial (-1.52 ± 0.13), and moss-covered (-2.68 ± 0.26) nests. (b) Experiment 2 with replicate samples on plots 1 and 2 (represented as P1 and P2, respectively). The loglinear slopes ± standard errors for the three nest types on plot 1 are: real (-3.52 ± 0.19), artificial (-1.14 ± 0.24), and moss-covered (-2.79 ± 0.25) nests. The loglinear slopes ± standard errors on plot 2 are: real (-2.74 ± 0.34), artificial (-1.53 ± 0.15), and moss-covered (-3.28 ± 0.06) nests. The loglinear slopes ± standard errors for the pooled replicates are: real (-3.19 ± 0.35), artificial (-1.31 ± 0.17), and moss-covered (-3.01 ± 0.20).

proximately 30-m intervals near the bottom of plot 1. Ten nests of each type were used with two quail eggs (*Coturnix coturnix*) per nest. Eggs were obtained from Department of Avian Sciences, University of California at Davis.

Experiment 2 used the three off-ground nest types described above plus three ground nest types. The first ground nest type was an artificial wicker nest that was lined on the inside with leaves and placed on top of the ground near the base of a plant stem (top nests hereafter). The second nest type was an artificial wicker nest, also lined with leaves, that was buried in the ground at the base of a maple stem such that the lip

of the nest was even with the ground and partially covered by dead leaves (buried nests hereafter). The third nest type was simply a small hole dug under a protruding maple stem (hole nests hereafter). Nests were placed at the base of maple stems to simulate nest placement by Orange-crowned Warblers (*Vermivora celata*), Virginia's Warblers (*V. virginiae*), and Red-faced Warblers (*Cardellina rubrifrons*) on the study sites (Martin, unpubl. data). Ten nests of each nest type were used with two eggs per nest on each plot; the six nest types were placed in sequential rotation along two transects established at the bottom or in the lower one-third of the sides of each drainage. Nests were placed at approximately 30-m intervals along each transect, with transects ranging from 25 to 70 m apart, depending on availability of suitable sites (i.e., small firs or maple thickets) for nest placement.

I attempted to place all nests in positions that reduced visual exposure to predators to minimize any confounding effects of differences in nest concealment on predation rates. Nests were checked every 3 to 5 days for a 15-day period; a 15-day period is similar to the combined egg-laying and incubation period of small passerines. I considered a nest to have been depredated when either the nest or one or both eggs were removed.

Number of nests remaining undepredated at each nest check was regressed against log-transformed numbers of days exposed plus 1.0; 1.0 was added to allow log-transformation of day 0. Because the intercept was fixed, the resulting slope represented the predation rate on a nest type; higher slopes indicated greater predation rates. Differences in predation rates (slopes) between replicates were tested using t-tests. Differences in predation rates (slopes) among nest types required multiple comparisons and, so, were tested by the least significant difference test using the mean square obtained from analysis of covariance.

RESULTS

COMPARISONS BETWEEN REPLICATES

Predation rates of off-ground nests did not differ between temporal replicates on plot 1 for artificial ($t = 1.41, P > 0.10$), moss ($t = 0.30, P > 0.50$), or real ($t = 0.07, P > 0.50$) nests (Fig. 1). Predation rates for off-ground nests also did not differ between spatial replicates on plots 1 and 2 for artificial ($t = 1.31, P > 0.20$), moss ($t = 1.70, P > 0.10$), or real ($t = 2.12, P > 0.05$) nests (Fig. 1b). However, predation rates for ground nests differed between spatial replicates for buried ($t = 2.62, P < 0.05$) and hole ($t = 2.81, P < 0.05$) nests, but did not differ for top nests ($t = 0.20, P > 0.50$).

OFF-GROUND NESTS

In experiment 1, the predation rate for artificial nests was lower than for real ($P < 0.001$, LSD = 1.82) and moss ($P < 0.05$, LSD = 0.92) nests, but predation rates for the latter two did not differ ($P > 0.05$, LSD = 0.92) (Fig. 1a). Replicates in experiment 2 were pooled because predation rates did not differ between replicates (see above). Again, the predation rate for artificial nests was lower than for moss ($P < 0.001$, LSD = 1.37) and real ($P < 0.001$, LSD = 1.37) nests, but predation rates for moss and real nests did not differ ($P > 0.05$, LSD = 0.92) (Fig. 1b).

GROUND NESTS

Because predation rates of buried and hole nests differed between spatial replicates (see above), replicates were analyzed separately. On plot 1, nests on top of the ground had a greater predation rate than buried ($P < 0.01$, LSD = 1.48) or hole ($P < 0.01$, LSD = 1.48) nests, but the latter two types did not differ ($P > 0.05$, LSD = 1.05) (Fig. 2a). On plot 2, predation rates did not differ between any of the nest types ($P > 0.05$, LSD = 1.56) (Fig. 2b).

OFF-GROUND VS. GROUND NESTS

My artificial and top nests are equivalent to the off-ground and top ground nest types, respectively, of previous studies (see Loiselle and Hoppes 1983, Wilcove 1985). The predation rate for nests placed on top of the ground was greater ($P < 0.01$, LSD = 1.00) than for artificial off-ground nests, but the predation rate for real off-ground nests was greater ($P < 0.05$, LSD = 0.74) than for these ground nests (Figs. 1, 2).

DISCUSSION

These experiments show that some results of nest predation experiments using artificial wicker nests are consistent. For example, nest predation rates were repeatable through time for all three off-ground nest types. Although not tested here, predation rates on ground nests should also be tested for temporal repeatability, especially given their variability in space.

However, these experiments also demonstrate that some definite biases are associated with the use of artificial wicker nests to test predation rates and that these biases are not necessarily consistent among nest types or areas. Results of the experiments using off-ground nests are particularly interesting and somewhat surprising. I expected artificial nests to suffer higher rates of predation because they are more conspicuous, at least to human observers. Instead, they suffered significantly lower predation rates than either real nests or artificial nests that were modified to resemble real nests (Fig. 1).

Observed differences in predation rates among the three types of off-ground nests seem to be due solely to differences in nest appearance. All nests were approached by investigators to check nest contents eliminating any differences due to human visitation. Chemical differences also seem unlikely; if predators find nests based on bird scent, then I would expect predators to find the real nests more frequently than the other nest types. Yet, artificial nests covered with moss to more closely simulate the appearance of real nests were attacked at very similar rates to real nests. Predators could not be responding to the smell of moss because it is abundant throughout the drainages. Thus, differences in rates of predation among the off-ground nest types seem to be due to differences in appearances, indicating that the main predators responding to these nest types are visually oriented and they develop search images for finding the nests.

The similar predation rates among the three ground nest types on plot 2 (Fig. 2b) could arise if predation was primarily by scent-oriented predators; if predators are attracted to nests with human scent, as suggested by some investigators (e.g., Snelling 1968, Nol and
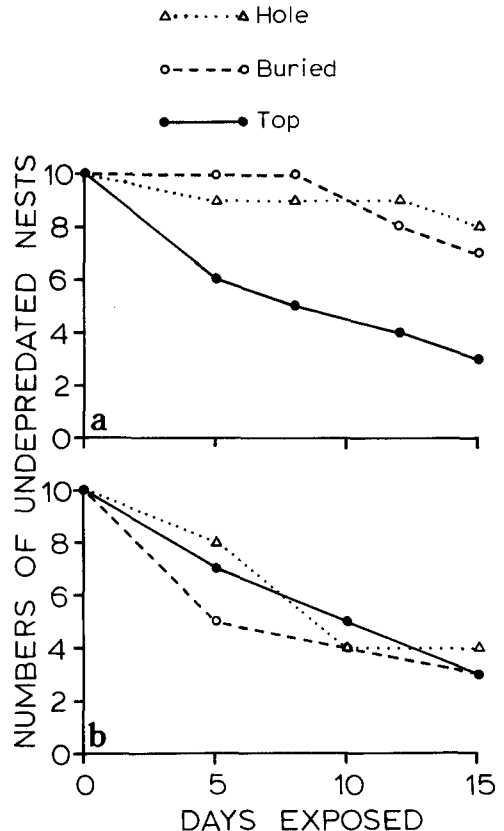

FIGURE 2. Numbers of undepredated nests relative to numbers of days exposed for ground nests. (a) Plot 1. The loglinear slopes ± standard errors for the three nest types are: nests on top of the ground (-2.43 ± 0.37), buried nests (-0.84 ± 0.56), and hole nests (-0.56 ± 0.17). (b) Plot 2. The loglinear slopes ± standard errors for the three nest types are: nests on top of the ground (-2.35 ± 0.43), buried nests (-2.52 ± 0.14), and hole nests (-2.26 ± 0.65). The loglinear slope ± standard error for pooled replicates for nests on top of the ground is -2.40 ± 0.18.

Brooks 1982), then differences in predation rates among nest types are not expected because all nest types were handled and checked by humans. Yet, predation rates were not similar among the three ground nest types on plot 1 (Fig. 2a). Such differences between plots potentially reflect differences in the types or abundances of predators and the means by which they detect nests (e.g., visual vs. olfactory).

Biases induced by nest appearance and differences among predators are most clearly expressed by comparisons of ground and off-ground nests. Both Loiselle and Hoppes (1983) and Wilcove (1985) concluded that predation rates were greater for ground nests than off-ground nests. When I use methods comparable to theirs (my artificial and top nest types), I obtain results similar to theirs. However, if I base the analysis on nests

that are more realistic in appearance (i.e., real nests for off-ground and buried or hole nests for the ground) then I obtain the opposite result; off-ground nests have higher predation rates than ground nests. Moreover, this latter trend is the one displayed by actual nests in this habitat (Martin, unpubl. data).

Of course, results of my study may not necessarily be comparable to those of earlier experiments due to differences in the identities of predators or in the types of actual nests with which predators are familiar. Nevertheless, my results certainly indicate that the potential biases caused by using artificial nests should be tested in future studies. Comparisons between areas probably should be restricted to a single nest type and data for different nest types should not be pooled; each nest type and position should be investigated separately because unique biases may exist for each of these.

Because different predators use different search tactics, predation rate comparisons among sites based on artificial nests should include careful consideration of differences in predators. This caution is particularly important in comparisons of predation rates among habitat islands. Wilcove (1985) and others (e.g., Matthiae and Stearns 1981, Whitcomb et al. 1981) have argued (without quantitative data) that types of predators differ among habitat islands as a function of area. Such systematic changes in types of predators with area can exert a marked effect on predation rates as measured by artificial nests due to differential responses of different predators to artificial nests. Attempts to more closely simulate appearances and positions of real nests may reduce such biases. However, even these nests do not measure actual predation rates on nests that are positioned and visited by birds rather than people. Direct determination of nest predators and their relative importance in nest predation is badly needed in future studies.

LITERATURE CITED

DUEBBERT, H. F., AND H. A. KANTRUD. 1974. Upland duck nesting related to land use and predator reduction. J. Wildl. Manage. 38:257–265.

LOISELLE, B. A., AND W. G. HOPPES. 1983. Nest predation in insular and mainland lowland rainforest in Panama. Condor 85:93–95.

MARTIN, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual, p. 181–210. In R. F. Johnston [ed.], Current ornithology. Vol. 4. Plenum Press, New York.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Ann. Rev. Ecol. Syst. 18:453–487.

MATTHIAE, P. E., AND F. STEARNS. 1981. Mammals in forest islands in southeastern Wisconsin, p. 55–66. In R. L. Burgess and D. M. Sharpe [eds.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15:167–175.

NOL, E., AND R. J. BROOKS. 1982. Effects of predator exclosures on nesting outcome of killdeer. J. Field Ornithol. 53:263–268.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1–48.

SAVIDGE, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–435.

SKUTCH, A. F. 1966. A breeding bird census and nesting success in Central America. Ibis 108:1–16.

SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54:159–169.

SNELLING, J. C. 1968. Overlap in feeding habits of Red-winged Blackbirds and Common Grackles nesting in a cattail marsh. Auk 85:560–585.

WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of eastern deciduous forest, p. 125–205. In R. L. Burgess and D. M. Sharpe [eds.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.