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DOES VERTICAL PARTITIONING OF NEST SITES DECREASE NEST PREDATION?

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ABSTRACT.—Partitioning of nest heights among co-occurring species in response to nest predation has been proposed as a process that helps to structure avian species assemblages. In the experiment reported here, we used artificial nests baited with Japanese Quail (*Coturnix japonica*) eggs to test (1) whether both rate and final level of nest predation differed among nests placed at ground, shrub, and tree strata; and (2) whether vertical partitioning of nest sites among the three strata decreased nest predation. Although rates of nest predation increased from ground, to partitioned, to shrub, to tree strata, the only significant pairwise differences were between predation on ground nests versus all other treatments. The proportion of nests depredated at the conclusion of the experiment was lowest for the ground treatment, intermediate for the partitioned treatment, and highest for the shrub and tree treatments. Predation was significantly higher in 1988 than in 1989, and significant variation in predation occurred among five spatial replicates of the experimental treatments. Although the results show different susceptibilities to nest predation according to vegetative stratum, they show only a slight and nonsignificant reduction in nest predation as a consequence of vertical nest-site partitioning. *Received 9 December 1998, accepted 1 October 1999.*

AVIAN ASSEMBLAGES have long been believed to be structured by biotic interactions, primarily competition for food (see Wiens 1989). Although competitive interactions may account for many patterns of species composition and abundance in natural communities (MacArthur 1972, Diamond 1978), other processes, particularly nest predation, have been suggested to structure bird assemblages (Martin 1988a, b; 1996). Nest predation is the major cause of nest failure for open-nesting birds (Ricklefs 1969, Martin 1993a). Predators can reduce fitness of adults by consistently taking eggs or nestlings (Ricklefs 1989). This in turn should select for birds to minimize the risk of nest predation (Martin 1988a, 1993b). Nest predation may be avoided or minimized in at least two ways: (1) by individual birds selecting cryptic nest sites (Hill 1984, Rands 1988); and (2) by each co-occurring species selecting sufficiently different nest sites, thereby reducing the probability that a particular nest is encountered by an individual predator (Martin1988a, Hoi and Winkler 1994, Schmidt and Whelan 1998). This latter mechanism, generated by the effects of shared predators among co-occurring species (apparent competition; Holt 1977), has been referred to as competition for enemy-free space (Jeffries and Lawton 1994).

We compared predation rates on artificial nests placed at one of three vegetative strata (ground, shrub, tree) to test whether predation at nests distributed among the three strata was lower than that at nests located within a single stratum. If predators respond to nests within a vertical stratum in a density-dependent manner, and if they respond to specific nest locations by forming search images (Martin 1988a,b; Ricklefs 1989), then predation should be higher in experimental plots in which nests are in a single stratum than in plots in which the same number of nests is dispersed among different strata. Although artificial nests do not exactly mimic nests of real birds (Major and Kendal 1996, Ortega et al. 1998, Wilson et al. 1998), and their use is associated with particular biases (Whelan et al. 1994, Major and Kendal 1996, Sloan et al. 1998), they can be used effectively for comparative purposes if the results they generate are interpreted with caution (e.g. Martin 1987, Yahner et al. 1989, Reitsma 1992, Roper 1992). In particular, if replicate plots do not differ substantially in the composition and abundance of their predator assemblages, artificial nests can help elucidate the relative vulnerability of nests that are placed in

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different macrohabitats or microhabitats, or that are exposed at different times within the breeding season (Sloan et al. 1998).

STUDY AREA AND METHODS

This study was conducted at the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. Hubbard Brook is in the southern portion of the White Mountain National Forest and consists of a largely contiguous and relatively homogeneous and unfragmented forest dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*; see Holmes et al. 1986). Artificial stick nests made of woven twigs (10 cm diameter, 5 cm depth) were baited with two Japanese Quail (*Coturnix japonica*) eggs. These nests more closely resembled real bird nests than the wicker nests that commonly have been used in artificial nest experiments (e.g. Loiselle and Hoppes 1983, Martin 1987, Whelan et al. 1994). Fifteen nests were placed 50 m apart on each plot in a 4 × 4 grid (minus one nest in a randomly selected intersection within the grid). The density of nests in the experiment (15 per 2.25 ha, or 6.7 per ha) corresponded closely to calculated densities of all natural nests of coexisting bird species on comparably sized plots at Hubbard Brook (16.1 nests per 2.25 ha, or 7.24 per ha; R. T. Holmes unpubl. data).

The experiment consisted of four nest-stratum treatments, with treatments replicated at five locations that were separated from one another by more than 1 km. Within a replicate location, the treatment plots were located more than 100 m from each other. The experimental design resulted in a total of 300 nests (4 treatments × 5 replicates × 15 nests). In the ground treatment, each nest was placed in a depression in the ground, resembling the nest site of a Hermit Thrush (*Catharus guttatus*). The nests were positioned by scooping out a depression of litter, placing a thin layer of leaf litter into the nest, and then putting the nest into the depression. In the shrub treatment, each nest was positioned in the fork of a shrub (mostly *Viburnum alnifolium*) between 0.25 to 1.5 m above ground, resembling the nest site of a Black-throated Blue Warbler (*Dendroica caerulescens*). In the tree treatment, each nest was placed in the crotch of a large sapling or tree formed by a branch with the main trunk (>5 m tall) between 2.5 to 8 m above the ground. This location resembled those used for nest sites by many of the breeding birds at Hubbard Brook, including the American Redstart (*Setophaga ruticilla*). In the partitioned treatment, five nests were placed at each of three strata, the stratum being randomly selected for each of 15 grid intersections. Regardless of treatment, each selected nest site was in what was judged to be an appropriate and well-concealed location within 10 m of a grid intersection, which in turn slightly decreased the uniformity of overall nest dispersion on each treatment plot.

The experiments were conducted from 20 June to 17 July 1988 and from 17 June to 9 July 1989, which corresponds to the breeding season at Hubbard Brook. We monitored nests on days 5, 10, and 15 after their placement in the forest. It was not possible to place all nests in a given year in the field on the same day, but all nests at a single location were placed on the same day. Nests were considered depredated if one or more eggs were destroyed or missing from the nest.

Ten cameras with trip devices (modified from Picman 1987) were used to photograph predators at artificial nests. The cameras were used opportunistically by placing them on plots with moderate to high amounts of predation after the 15 days of nest monitoring. If an egg was removed from a nest that had a camera attached, we placed a new egg in the nest up to three times to increase the probability of obtaining a clear photograph. Cameras were moved to different locations within and among plots in an attempt to identify the nest predators in different areas, but because of the small number of cameras, plots with low predation were not monitored.

We evaluated results in two complementary analyses. First, the rate at which eggs were depredated was analyzed with survival (or failure time) analysis (Pyke and Thompson 1986, Whelan et al. 1994). We tested for differences among nest-stratum treatments, between years, and among replicate plots. We used a Breslow-Gehan test (a generalized Kuskal-Wallis test that yields a χ^2-value for comparing K samples), which places greater weight on predation events early in the experiment when sample sizes are largest (Breslow 1970, Steinberg et al. 1997). An analysis that yielded a significant overall difference in rates of predation among the four treatments was followed by multiple comparisons of each pairwise combination of the four strata (Bonferonni-corrected level of significance = 0.008). Second, the proportion of nests in each treatment surviving until the end of the experiment was compared with ANOVA (following arcsine-square root transformation) in which the model included the main effects of treatment, location, and year, as well as the interaction of treatment and year. Significant differences in means were determined with Fisher's LSD post-hoc comparison ($\alpha = 0.05$).

Owing to the smaller number of nests within each stratum in the partitioned treatment when compared with that in each "companion" treatment (e.g. nests placed on the ground in the partitioned treatment vs. nests in the ground-only treatment), we declined to statistically compare the proportion of nests depredated between the treatments. Instead, we simply report the mean proportion (± SE) of nests that was depredated for each stratum treatment and by stratum for the partitioned treatment.

RESULTS

Rates of nest predation differed significantly among the treatment strata ($\chi^2 = 35.48$, df = 3, $P < 0.001$), with the rate increasing among experimental treatments from ground, to partitioned, to shrub, to tree strata (Fig. 1A). Pairwise comparisons indicated that nests in the ground stratum experienced a significantly lower rate of predation than all other treatments (all $\chi^2 > 15$, df = 1, all $P < 0.001$). Rates of predation did not differ significantly among any of the other treatments.

The rate of predation was significantly higher in 1989 than in 1988 irrespective of treatment strata and location ($\chi^2 = 31.24$, df = 1, $P < 0.001$; Fig. 1B), and predation rate also differed significantly among treatment locations irrespective of treatment strata and year ($\chi^2 = 44.87$, df = 4, $P < 0.001$; Fig. 1C).

The proportion of nests depredated at the end of the experiment was significantly affected by treatment ($F = 3.31$, df = 3 and 28, $P = 0.034$) and year ($F = 5.5$, df = 1 and 28, $P = 0.026$). Neither location ($F = 2.47$, df = 4 and 28, $P = 0.067$) nor the treatment × year interaction ($F = 0.36$, df = 3 and 28, $P = 0.783$) had significant effects on nest predation. The ground stratum had the lowest proportion of nests depredated, the partitioned treatment was intermediate, and the shrub and tree strata had the highest proportion of nests depredated (Fig. 2). Overall, nest predation in 1989 (53 ± SE of 6.2%) was almost twice that in 1988 (30.7 ± 6.2%).

Within the partitioned treatment, the proportion of nests depredated within the ground and shrub strata increased slightly over that for the respective companion treatment (ground, 0.28 ± 0.07 vs. 0.21 ± 0.053; shrub, 0.50 ± 0.11 vs. 0.49 ± 0.12), whereas the proportion of nests depredated within the tree stratum decreased slightly below that for the companion treatment (0.46 ± 0.14 vs. 0.53 ± 0.12).

The presence or absence of particular predators at the different treatment strata documented by the trip cameras included: 12 photographs of deer mice (*Peromyscus* sp.), 11 of red squirrels (*Tamiasciurus hudsonicus*), 4 of Blue Jays (*Cyanocitta cristata*), 2 of woodland jumping mice (*Napaeozapus insignis*), 1 of a raccoon (*Procyon lotor*), and 1 of a black bear (*Ursus americanus*). Deer mice and red squirrels were

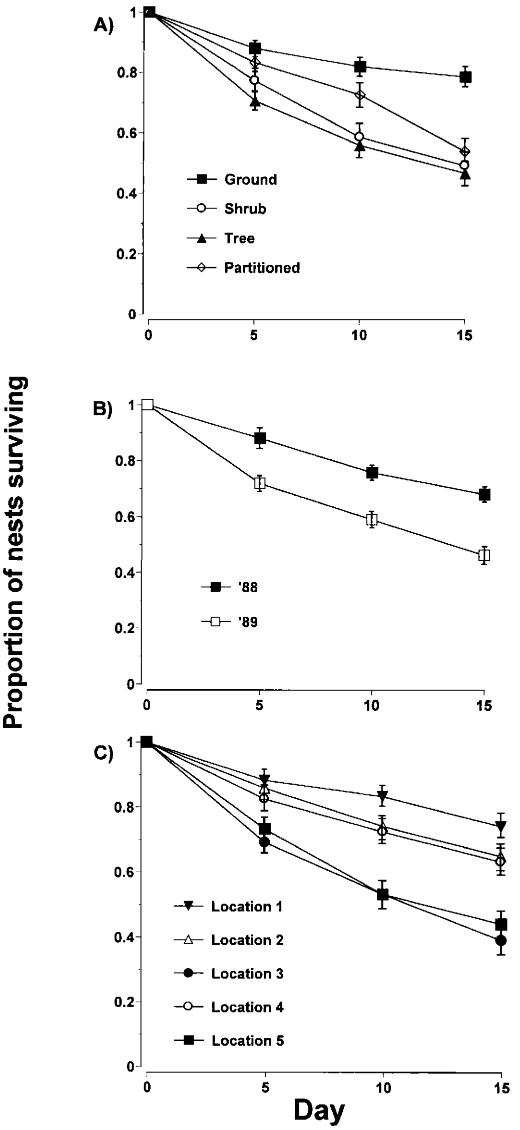

FIG. 1. Mean proportion (± SE) of nests surviving 15-day experiment examining nest predation on nests located in one of three vertical vegetative strata or partitioned among the three strata. (A) Survival curves for nests located on the ground, shrub, or tree strata, or partitioned among them, pooling results for five replicate plots (locations) of each treatment and year (1988 and 1989). (B) Survival curves for experimental nests in 1988 and 1989, pooling results for treatment (stratum) and location (replicate). (C) Survival curves for the five replicate locations, pooling results for treatment (stratum) and year.

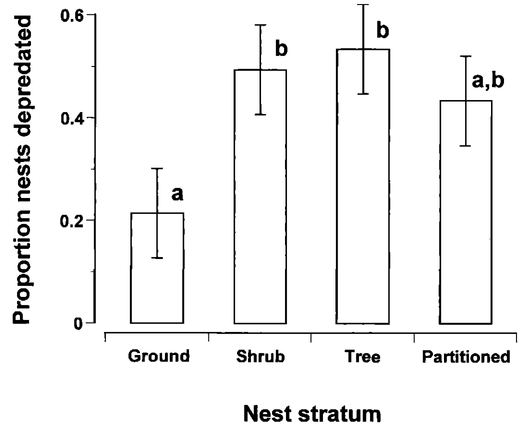

FIG 2. Mean proportion (± SE) of nests depredated when located in the ground, shrub, or tree strata, or partitioned among them, at the final census (day 15) of experiment. Results are pooled over five replicates of each treatment (stratum) and over the years 1988 and 1989. Different letters above bars indicate significant differences (Fisher's LSD test, $\alpha = 0.05$).

photographed at plots of each nest-stratum treatment. Woodland jumping mice, the raccoon, and the black bear were photographed only at the shrub treatment. Blue Jays were photographed only at the tree treatment and on plots in which almost all tree nests were depredated.

DISCUSSION

This experiment demonstrated that artificial nests placed on the ground in this northern hardwoods forest are depredated at lower rates and to a lesser extent than those placed in shrubs or trees (see Sloan et al. 1998). This result is in agreement with established patterns of nest predation noted in literature reviews (Martin 1993b, 1995) and with studies elsewhere using nest simulations on and above the ground, both with (Yahner et al. 1989) and without (Nilsson et al. 1985) artificial nests. Because no detailed studies have been conducted on the reproductive ecology of ground-nesting birds at Hubbard Brook, it is difficult to determine whether the finding of reduced predation intensity on ground nests reflects that for natural nests. Furthermore, the rate and extent of predation in the treatment that partitioned nests among the three strata also were higher than those for nests placed only on the ground stratum. However, the rate and the extent of predation also varied with year and plot location irrespective of vegetative stratum. In general, although our results indicated different vulnerability to nest predation at different vegetative strata, they were not consistent with the hypothesis that partitioning nests among the strata reduces predation.

The high spatial and temporal variability in nest predation for both shrub and tree nests is an important finding considering the potential importance of nest predation as a selective pressure in organizing avian assemblages. As documented by the nest cameras, Hubbard Brook has a variety of nest predators. Although not all predators were photographed in all strata and at each test location, most, if not all, of these predators are known to depredate nests in all strata (Schmidt and Whelan 1999a, L. R. Reitsma unpubl. data). In addition to those photographed in this study, predators include eastern chipmunk (*Tamias striatus*), Sharp-shinned Hawk (*Accipiter striatus*), fisher (*Martes pennanti*), and possibly other small mammals (Reitsma et al. 1990, Sloan et al. 1998, R. T. Holmes unpubl. data). These predators vary in many respects, from foraging strategy to home-range size. It seems plausible that their different spatial and temporal activity patterns may contribute to differences in the rate and extent of nest predation among the different plot locations of the experimental treatments.

The potential for nest predation to structure avian assemblages relies on the mechanism of density dependence (Martin 1988a, Ricklefs 1989). In another artificial nest experiment conducted at Hubbard Brook, Reitsma (1992) found no evidence for density-dependent nest predation when all nests were placed within the low shrub stratum. Although density-dependent nest predation has been documented in numerous studies (e.g. Perrins 1965, Krebs 1971, Nilsson et al. 1985), others have found nest predation to be density independent (Gottfried 1978, Blancher and Robertson 1985, Hannon et al. 1988), and one study documented both density-dependent and density-independent nest predation at a single location within a given breeding season and for different vegetative strata (Schmidt and Whelan 1999a). Whether nest predation is density dependent will depend on many factors, including characteristics of co-occurring nesting species, composition of the predator assemblage, structure of the habitat, and abundance and distribution of alternative food resources for the nesting species and their predators (Ricklefs 1989, DeGraaf 1995, Schmidt and Whelan 1999a).

As pointed out by Ricklefs (1989), the core of Martin's arguments can be recast in the framework of consumer-mediated coexistence owing to apostatic selection (resulting from frequency-dependent predation; see also Hoi and Winkler 1994). That is, when bird species nest in different vegetative strata and/or in different microhabitats within a given stratum (e.g. proximal vs. distal portions of branches), nest frequency as well as density may vary among strata, even if overall density remains constant per unit area. If nest-site selection (microsites within a stratum or use of sites among strata) is considered to be an evolutionary strategy, it may be useful to conceptualize nest-site selection as an ecological and evolutionary game (e.g. Vincent and Brown 1988; Brown 1990; Schmidt and Whelan 1998, 1999b). From this perspective, the players are the co-occurring nesting species and their potential nest predators. From the perspective of evolutionary game theory, the fitness payoffs for nesting in a particular stratum (or microhabitat type within a stratum) will depend on the frequency with which co-occurring individuals (within and among species) select different nest sites, the defense (e.g. vigilance) and other behaviors (e.g. provisioning of incubating females by males, or of young by the pair) of nesting pairs, and the forging costs and strategies (cursorial vs. aerial, olfactory vs. visual, active vs. incidental; see Schmidt 1998, 1999; Schmidt and Whelan 1999b) of the resident predators.

The conclusions we can draw from this study must be tempered because we used artificial nests without a simultaneous study of natural nests with which to compare the results (see Schmidt and Whelan 1998, 1999a; Sloan et al. 1998). As suggested by Major and Kendal (1996) and Sloan et al. (1998), however, we used cameras to determine the identity of predators. Nonetheless, we believe that our results are illuminating. As in many other studies, we found that predation rates on ground nests were lower than those for nests in vegetation above the ground. We found that predation was not reduced when nests were held at a constant plot-wide density but partitioned among three vegetative strata, casting doubt on the efficacy of nest-site partitioning as a means to reduce nest predation. However, we also found that predation varied significantly in time and space. The spatial variability appeared to be related to differences in predator types among plot locations, and the temporal variability may have reflected differences in predator abundance (e.g Reitsma et al. 1990). Such variability simply may decrease (but not eliminate) the strength of selection for nest-site partitioning exerted by nest predation. If so, relatively long-term studies with large sample sizes (e.g. Martin 1996) or an accumulation of "independent samples of species assemblages . . . to gain statistical control" (Ricklefs 1989:186) may be necessary to demonstrate an effect of nest-site partitioning on nest predation.

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