PREDATION OF ARTIFICIAL NESTS IN HARDWOOD FRAGMENTS ENCLOSED BY PINE AND AGRICULTURAL HABITATS

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Abstract: Nesting success of songbirds often is poor in edge-dominated habitats. Because the spatial juxtaposition of forest fragments relative to other habitats may influence nest success, we tested the hypothesis that the depredation rate for bird nests in small hardwood forests would decrease if the degree of edge contrast with adjoining habitats was reduced. Over 4 trials, we placed 672 artificial nests (336 each at shrub and ground levels divided equally between edge and interior locations) in small (range = 0.5–5.0 ha) hardwood forest stands enclosed by either agricultural fields (n = 7) or mature pine forest (n = 7). Nest predation was greater (P = 0.001) in field-enclosed stands (35%) than in pine-enclosed stands (20%) because of greater (P = 0.03) predation of shrub nests. No differences ($P > 0.05$) in predation rates were detected between stand types for ground nests or between strata (i.e., ground nests vs. shrub nests) within field-enclosed stands. Predation rates did not differ ($P > 0.05$) between edge and interior nests between or within stand types. Nest predation by avian species was not suspected in pine-enclosed stands (0%), but 18% of the nests depredated in agriculture-enclosed stands was attributed to birds. The low edge contrast associated with pine-enclosed stands appeared to attract fewer nest predators, especially those that preyed on shrub nests. However, the value of lower predation rates for shrub nests in pine-enclosed stands may be offset by the presence of fewer shrub-nesting sites relative to similar-sized field-enclosed stands, because understory development was impoverished, probably as a result of reduced sunlight penetration.

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Recent evidence suggests forest fragmentation negatively affects nesting success of some songbirds (Brittingham and Temple 1983, Martin 1993). As forests are fragmented, the proportion of edge to interior habitat increases, and rates of predation and brood parasitism may rise. Terborgh (1989) noted that small predators often are especially abundant in small forest fragments, and edge habitats of small fragments also may support greater densities of avian nest predators than forest interior habitats (Whitcomb et al. 1981). Consequently, nest success of some songbirds often is poor in edge-dominated habitats (Gates and Gysel 1978).

Spatial distribution of forest fragments relative to other habitats may influence nest success. Wilcove (1985) reported that artificial nests in suburban fragments were depredated more frequently than nests in rural fragments, probably because of greater predator densities associated with human habitation. In Pennsylvania, Yahner and Scott (1988) reported highest nest predation in fragments adjoined by the largest percentage of clearcut land. Birds breeding in small forests sometimes incorporate adjacent nonagricultural habitat (i.e., second growth or other forest fragments) into their territories (Blake and Karr 1987). Therefore, nesting success in small forest fragments may be improved if other forest types or more suitable habitats exist nearby.

In South Carolina, pinelands compose roughly 28% of the land area (Tansey and Hutchins 1988); hence, many hardwood forest fragments are adjacent to, or surrounded by, pine forest. When a forest fragment is surrounded by intensively managed timberland, the functional size of the fragment may be increased, and the negative effects associated with forest fragmentation may be lessened because the edge contrast between the fragment and the adjoining habitat is diminished (Harris 1984, Kilgo et al. 1997). We tested the hypothesis that the depredation rate for bird nests in small hardwood forest

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fragments would decrease if the degree of edge contrast with adjoining habitats was reduced. We tested this hypothesis by comparing predation rates on artificial nests in hardwood stands surrounded by either agricultural fields or mature pine forest.

STUDY AREA

We located 7 hardwood stands surrounded by pine forest (pine-enclosed stands; PES) on the Savannah River Site (SRS) in the Upper Coastal Plain of South Carolina. Stands ranged from 0.5 to 5.0 ha and included mature oaks (*Quercus* spp.), mockernut hickory (*Carya tomentosa*), and black cherry (*Prunus serotina*). Mid- and understory species consisted of flowering dogwood (*Cornus florida*) and American holly (*Ilex opaca*), and shrubs and vines of the genera *Rubus* and *Vaccinium*. The pine forest matrix was ≥50 m in width and consisted of mature loblolly pine (*Pinus taeda*) or longleaf pine (*Pinus palustris*). We selected 7 stands isolated by a gap ≥30 m wide from contiguous forested habitat (field-enclosed stands; FES) in Barnwell and Allendale counties, southeast of the SRS. The stands were similar in size and species composition to those on the SRS and were surrounded by pasture or crop fields. We used the techniques of James and Shugart (1970) to sample vegetation in 3 0.04-ha plots for stands 0.5–1.9 ha, and in 5 plots for stands ≥2.0 ha.

METHODS

Experimental Design

We placed 12 artificial nests (10.0- × 6.0-cm wicker nests) in each stand, each nest containing 2 fresh Japanese quail (*Coturnix coturnix*) eggs (n = 168 nests/trial). In each stand, we placed 3 nests at each of 4 locations: (1) shrub-edge, (2) shrub-interior, (3) ground-edge, and (4) ground-interior. We placed edge nests <10 m from the stand edge, and we placed interior nests >25 m from the stand edge (Yahner and Wright 1985). All nests were spaced ≥15 m apart (Small and Hunter 1988), and nests located in similar strata generally were separated by greater distances.

We selected nest locations that resembled those of the species nesting in our study sites. We tied shrub nests in saplings, shrubs, or the lower branches of trees, 1.0–1.5 m aboveground. We placed ground nests in a depression at the base of saplings, shrubs, stumps, or under dead branches. We marked each nest with flagging tape >3 m from the nest site. We checked and retrieved nests 5 days after placement and placed them in new locations 6–8 days later. We repeated this procedure during 4 trials from June to July 1993. We wore rubber boots and gloves when handling nests and eggs to minimize human scent.

When feasible, we identified nest predators by appearance of eggs and nests (Rearden 1951, Best and Stauffer 1980). We considered eggs containing bill-shaped punctures to be depredated by birds. In instances where we found small egg fragments, we assumed predation by mammals. We considered the predator unknown when nests were found empty. We recorded nests as depredated if 1 or both eggs were damaged or missing, or if the nest had been overturned (Wilcove 1985, Rudnicky and Hunter 1993).

We pooled nest data across 7 stands per nest location per trial (n = 21; 7 × 3) and computed the percentage of depredated nests. Nests within stands were considered independent. Percentage data were arcsine transformed before statistical analysis. We tested the data for normality and equality of variance assumptions. We used 2-sample t-tests to compare ground coverage, canopy coverage, shrub density, and basal area of stems ≥3 cm diameter at breast height (dbh) between treatments (i.e., FES, PES). Differences in predation rates were tested for via a 2-factor analysis of variance, where factor 1 compared the effect of stand type (2 categories), and factor 2 compared the effect of nest location (4 categories). The unit of replication was the trial (n = 4). We conducted separate tests to evaluate the presence of a treatment effect, a nest location effect, and their interaction. We compared means using Tukey's w procedure.

RESULTS

Mean shrub density was greater (t_{12} = 2.06, P = 0.06) in FES (41,066 stems/ha) than in PES (21,074 stems/ha). No other differences in vegetation parameters were detected between treatments (canopy coverage: t_{12} = 0.91, P = 0.38; ground coverage: t_{12} = 1.74, P = 0.11; basal area of stems ≥3 cm dbh: t_{12} = 0.28, P = 0.79). Canopy coverage was 89% for PES and 91% for FES, and ground coverage was 55% for PES and 44% for FES. Stem basal area was 27 m²/ha for PES and 28 m²/ha for FES.

Nest predation differed among trials ($F_{3,31}$ =

Table 1. Percentage of artificial nests depredated, by trial and location, in 7 hardwood forest fragments enclosed by agricultural habitats (FES) and 7 hardwood fragments enclosed by pine forest (PES) in Aiken, Allendale, and Barnwell counties, South Carolina, 1993.

Stand type	Nest location	Trial 1	Trial 2	Trial 3	Trial 4	$\bar{x}$[a]	SE
FES	Ground-edge[b]	28.6	9.5	38.1	42.9	29.8A	7.4
	Shrub-edge	23.8	33.3	38.1	47.6	35.7A	5.0
	Ground-interior	19.1	42.9	28.6	71.4	40.5A	11.4
	Shrub-interior	33.3	28.6	38.1	42.9	35.7A	3.1
PES	Ground-edge	28.6	23.8	42.9	47.6	35.7A	5.7
	Shrub-edge	9.5	0.0	0.0	19.1	7.1B	4.6
	Ground-interior	14.3	23.8	38.1	33.3	27.4A	5.3
	Shrub-interior	9.5	9.5	4.8	9.5	8.3B	1.2

[a] Means followed by the same letter are not different ($P > 0.05$).
[b] Twenty-one nests were included in each location category, 3/forest fragment.

3.37, $P = 0.03$), with Trial 4 being greater than Trial 2, reflecting the increase in predation over the last 2 trials, particularly for nests in FES (Table 1). Mean predation rate was greater ($F_{1,31} = 22.55$, $P = 0.001$) for all nests in FES (35%) than PES (20%). This difference was caused by the greater ($F_{1,15} = 38.26$, $P < 0.001$) predation rate for shrub nests in FES than in PES. No differences in predation rates were detected between treatments for ground nests ($F_{1,15} = 0.12$, $P = 0.73$) or between strata within FES ($F_{1,15} = 0.06$, $P = 0.80$). However, within PES, predation rate for ground nests was greater ($F_{1,15} = 23.76$, $P < 0.001$) than that of shrub nests. No differences in predation rates were detected between edge and interior nests between ($F_{1,31} = 0.02$, $P = 0.88$) or within treatments (PES: $F_{1,15} = 0.22$, $P = 0.65$; FES: $F_{1,15} = 0.59$, $P = 0.45$).

We estimate that mammalian predators accounted for 67% of the nests depredated in PES and 27% of those in FES (Table 2). However, 55% of nests depredated in FES could not be assigned to a category. Nest predation by avian predators was not suspected in PES, but 18% of those depredated in FES were attributed to birds, and 82% of these nests were located in shrubs.

Table 2. Number of nests depredated, by nest location and predator category, in 7 hardwood fragments enclosed by agricultural habitats (FES) and 7 hardwood fragments enclosed by pine forest (PES) in Aiken, Allendale, and Barnwell counties, South Carolina, 1993.

Stand type	Nest location	Predator category: Bird	Mammal	Unknown
FES	Ground-edge	3	8	14
	Shrub-edge	7	3	20
	Ground-interior	1	19	15
	Shrub-interior	11	2	17
PES	Ground-edge	0	20	9
	Shrub-edge	0	4	2
	Ground-interior	0	20	4
	Shrub-interior	0	0	7

DISCUSSION

Experiments using Japanese quail eggs may bias estimates of predation rates for songbird nests because small mammals may not be able to consume the relatively larger quail eggs (Haskell 1995). Thus, results from studies using artificial nests should be interpreted with caution. However, if artificial nests are handled similarly among treatments, then the results can be valuable as a tool for comparative questions.

Nest predation is the principal source of nest failure for most passerine species, often causing losses in excess of 50% and occasionally exceeding 80% (Ricklefs 1969, Martin 1992). Predation rates in our study (7.1–40.5%) generally were lower than those reported for passerines and for similar experiments in forest fragments (Nilsson et al. 1985, Wilcove 1985, Small and Hunter 1988, Reitsma et al. 1990, Rudnicky and Hunter 1993, Seitz and Zegers 1993). However, they were similar to the apparent predation rates (27–40%) on real nests (northern cardinals [*Cardinalis cardinalis*]) in the same sites (Sargent 1996). Furthermore, the greater predation rates recorded in the last trial relative to earlier trials suggest predators became more efficient at locating nests. At least 2 features of our experiment may have reduced nest predation relative to other studies: (1) predators could not focus on bird activity to locate nests, and (2) the 5-day interval for each trial was ≤one-half the normal incubation interval of

most forest songbirds. We selected this abbreviated "incubation interval" because we were concerned that eggs would spoil, thus attracting predators.

The similar predation rates for edge and interior nests in each stand suggest there was no functional difference between edge and interior habitats in these stands. High nest predation rates characteristic of edge habitats may extend 300–600 m into a forest (Wilcove 1985), and no edge-related differences in predation may exist in some habitats (Yahner and Wright 1985, Angelstam 1986). Thus, small hardwood forests, like those in our study (0.5–5.0 ha), may have no true forest interior conditions (Brittingham and Temple 1983).

Nests in structurally complex habitats may suffer lower predation rates than nests in less complex habitats because complex habitats contain more potential nest sites for predators to search (Bowman and Harris 1980). However, shrub densities were highest in our FES (i.e., FES were structurally complex), yet predation rates for shrub nests also were highest in FES. Similarly, Yahner and Scott (1988) found that predation of shrub nests was highest in fragments bordered by 50% clearcut land and lowest in contiguous forest. In their study, corvids were the main predators on shrub nests. Although we have no data on snake and mammalian densities in our study sites, blue jays (*Cyanocitta cristata*) and American crows (*Corvus brachyrhynchos*) were detected nearly twice as often in FES as in PES (J. C. Kilgo, unpublished data). Also, it is likely that snakes and avian predators combined accounted for considerably more depredated nests in FES than the 18% attributed to birds. Wray and Whitmore (1979) recorded snakes and birds as nest predators for depredated nests in which the nest appeared undisturbed, and 55% of the nest losses in FES were attributed to unknown predators (i.e., undisturbed nests). Thus, despite their more complex understory structure, FES appeared to be attractive to visual predators such as birds. Yahner et al. (1989) noted that avian nest predators such as corvids often perch along the abrupt ecotone between forested and unforested land (i.e., a "hard edge"). Thus, our results suggest arboreal nests in small isolated forests may be particularly vulnerable to avian predators concentrated along these hard edges, regardless of the structural complexity of the habitat within the forest stand.

Yahner et al. (1989) detected no relation between edge contrast and depredation rate for artificial nests placed at the interfaces of mature forest stands and 2- or 12-year-old edges. These authors concluded that the nest success of birds, especially arboreal nesting species, was more negatively affected by the amount of edge in the landscape than degree of edge contrast. However, Harris (1984) noted that effective size of a forest fragment may be increased if the degree of habitat difference (i.e., contrast) between that fragment and the adjoining matrix is small (i.e., a "soft edge"). Densities of nest predators in small hardwood fragments enclosed by mature pine forest probably are low because these sites often are structurally simple and contain no hard edges. The structural simplicity of these sites may result from the poor light penetration allowed by the closed canopy pine forest adjacent to the hardwood fragment. In our study, depredation rates for nests located in shrubs were highest in FES, possibly because species that prey on arboreal nests are more common in these hard-edged sites. In contrast, the soft-edged PES may have attracted fewer species that prey on arboreal nests, possibly because PES edges lack the structural diversity of FES. However, the value of lower predation rates for shrub nests in PES may be offset by the presence of fewer shrubs (i.e., fewer potential nesting sites) relative to similar-sized FES.

MANAGEMENT IMPLICATIONS

Management prescriptions that include maintenance of a pine forest buffer surrounding small hardwood forest stands should benefit shrub-nesting birds. Nest predation rates in our study were greater in stands lacking such a buffer. Similarly, Kilgo et al. (1997) determined that forest-interior Neotropical migrants nesting in small hardwood stands may benefit from the presence of an adjacent, closed-canopy pine forest. Future research should address appropriate widths for buffer zones.

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