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## NEST PREDATION IN FOREST TRACTS AND THE DECLINE OF MIGRATORY SONGBIRDS<sup>1</sup>

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**Abstract.** Nest predation has been suggested as an important cause of the decline of breeding populations of migratory songbirds in small woodlots in eastern North America. I tested this hypothesis by placing artificial nests with fresh quail eggs in forests of different sizes in Maryland and Tennessee. Predation rates were higher in small woodlots than in large tracts. Predation was especially intense in woodlots near suburban neighborhoods compared to woodlots in isolated rural areas. Experimental open-cup nests were more vulnerable to predators when placed on the ground vs. 1–2 m above ground. In either position these open-cup nests were more vulnerable to predators than experimental cavity nests. Since most species of migratory songbirds construct open-cup nests, and several species place them near the ground, migratory songbirds should be strongly affected by higher predation rates in small forest tracts.

**Key words:** cavity nests; extinction; migratory songbirds; neotropical migrants; nest predation; open-cup nests; woodlots.

### INTRODUCTION

The loss of species from habitat islands is well documented, but in most cases the cause of the extinction is unknown. This is certainly true for the avifauna of the eastern deciduous forest of North America, where breeding populations of passerines have been declining or disappearing in small forest tracts. Forest-dwelling species that winter in the Neotropics have been affected most dramatically (Robbins 1979, Whitcomb et al. 1981). A number of causes have been suggested for these declines, including: brood parasitism by the Brown-headed Cowbird, *Molothrus ater* (Brittingham and Temple 1983), the loss of winter habitat in Latin America (Briggs and Criswell 1979, Ambuel and Temple 1982), a low rate of colonization and a high rate of extinction in small, isolated woodlots (Whitcomb et al. 1981), the lack of critical microhabitats (Lynch and Whigham 1984) or food resources (Blake 1983) in small tracts, and higher rates of nest predation in small woodlots compared to large forest tracts (Robbins 1980, Ambuel and Temple 1983). To date, however, differential rates of predation have not been documented. Here I report experiments that show higher rates of nest predation to be characteristic of small forest tracts. These results indicate that nest predation is an important cause of the decline of neotropical migrants.

### METHODS

My study sites were 10 forest tracts in central Maryland (3.8–905 ha) and one in southeastern Tennessee (Great Smoky Mountains National Park, 209 000 ha) (Table 1). Although  $\approx 675$  km farther south and 900 m higher in elevation than the Maryland sites, the Great Smoky Mountains was included for three reasons: (1) it contains the most extensive tract of virgin

forest in the eastern United States; (2) it retains forest-dwelling mammals and birds that have long been extirpated from central Maryland, including mountain lion (*Felis concolor*), bobcat (*Lynx rufus*), black bear (*Ursus americanus*), Cooper's Hawk (*Accipiter cooperii*), Wild Turkey (*Meleagris gallopavo*), and Ruffed Grouse (*Bonasa umbellus*); (3) the Smoky Mountains and central Maryland share many of the same nest predators. These include raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), eastern chipmunk (*Tamias striatus*), gray squirrel (*Sciurus carolinensis*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), and several species of snakes. The Maryland sites included two large tracts (905 and 283 ha) and eight small woodlots (3.8–13.3 ha). I followed Whitcomb et al. (1981) and divided the small woodlots into two groups: those surrounded by housing developments ("suburban"), and those surrounded by agricultural fields ("rural").

Bird surveys in the Smoky Mountains (D. Wilcove, *personal observation*) and the two large Maryland tracts (Whitcomb et al. 1981, D. Wilcove, *personal observation*) confirmed the presence of most of the local forest-dwelling neotropical migrants. Species missing from all or most of the small woodlots (Whitcomb et al. 1981, D. Wilcove, *personal observation*) included: Veery (*Catharus fuscescens*), Yellow-throated Vireo (*Vireo flavifrons*), Northern Parula (*Parula americana*), Black-and-white Warbler (*Mniotilta varia*), Worm-eating Warbler (*Helmitheros vermivorus*), Ovenbird (*Seiurus aurocapillus*), Kentucky Warbler (*Oporornis formosus*), Hooded Warbler (*Wilsonia citrina*), and Scarlet Tanager (*Piranga olivacea*).

To measure the amount of predation, I placed artificial nests each with three fresh quail eggs in the forest tracts between 6 June and 5 August 1983. This experimental procedure was modelled after that of Loiselle

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TABLE 1. Area, location, elevation, and vegetation of the sites where experimental nest predation studies were conducted.

Tract	Area (ha)	Location	Elevation (m)	Forest type
<b>Large tracts</b>				
A	209 000	Great Smoky Mountains National Park, Sevier County, Tennessee T1: 35°42'31" N, 83°20'32" W* T2: 35°41'44" N, 83°27'48" W*	1079–1085 897–909	oak hemlock-beech
B	905	National Agricultural Research Center, Prince George's County, Maryland T1: 39°02'02" N, 76°49'20" W* T2: 39°00'45" N, 76°50'45" W*	49–61 36–43	oak-pine oak-hickory
C	283	Montgomery County, Maryland 39°07'53" N, 76°55'27" W	91–122	oak-hickory
<b>Rural woodlots</b>				
D	11.7	Prince George's County, Maryland 39°01'00" N, 76°49'18" W	43–55	oak-black gum
E	8.8	Montgomery County, Maryland 39°13'08" N, 77°10'41" W	134–146	oak
F	3.8	Montgomery County, Maryland 39°14'49" N, 77°09'28" W	165–170	oak-hickory-tuliptree
G	3.8	Montgomery County, Maryland 39°11'15" N, 77°02'53" W	116–122	oak-hickory-tuliptree
<b>Suburban woodlots</b>				
H	13.3	Prince George's County, Maryland 39°03'00" N, 76°57'05" W	82–94	oak
I	7.4	Montgomery County, Maryland 39°05'24" N, 77°01'40" W	113–125	oak-tuliptree
J	4.2	Prince George's County, Maryland 39°01'37" N, 76°55'35" W	40–52	oak-pine
K	3.8	Montgomery County, Maryland 39°04'42" N, 77°02'40" W	98–110	oak-tuliptree

\* T1 and T2 denote the widely separated transects used in the two largest tracts.

and Hoppes (1983). The nests were straw-colored, wicker baskets of the type used by aviculturists. They were shaped like an open-cup nest, measuring 100 mm (diameter) by 60 mm (depth). I lined them with straw but made no other attempt to simulate a natural appearance. The eggs came from Japanese Quail, *Coturnix coturnix*, and averaged 28 × 23 mm in size. They were cream-colored with varying amounts of brown or black speckling. Nests were placed at 25-m intervals 5–10 m from a transect line through each tract. Within each of the two largest tracts (209 000 and 905 ha) I placed the nests along two widely separated transect lines.

To determine whether nest position affected the likelihood of predation, within each tract I placed nests alternately at the bases of trees and shrubs ("ground nests") and 1–2 m above the ground in shrubs and saplings ("above-ground nests"). Nests were checked after 7 d, and those that had lost one or more eggs were counted as preyed upon. In four of the Maryland tracts (B, G, I, J) I repeated the experiments to assess local variability in predation.

For each woodlot I referred to the percentage of experimental nests lost to predators after 7 d as the "predation rate" of that woodlot. However, comparisons of the predation rates in different woodlots actually

involved comparisons of the numbers of preyed upon vs. undisturbed nests. These comparisons were made using the  $\chi^2$  Contingency test (with one degree of freedom) and the Fisher Exact Probability test (both tests two-tailed).

The experimental nests were more conspicuous than the actual nests of migratory passerines. Thus, while this experiment could measure the relative magnitude of predation in forest tracts of different sizes, it could not measure the actual rate of predation that the birds were experiencing.

From 19 June to 26 July 1984, I identified some of the nest predators by track sampling. I placed cardboard squares (20.3 × 20.3 cm), lightly coated with a black masonry dry color and misted with hair spray, next to artificial ground nests. The nests were checked daily, and, where possible, the identities of the predators determined from tracks left on the cardboard. I used this technique in two rural (E, G) and two suburban (I, J) woodlots.

To learn which types of nests are most vulnerable to predators, I compared the amount of predation on experimental cavity nests vs. wicker open-cup nests. I constructed the cavity nests by hollowing out 20–30 cm sections of small tree trunks. In each trunk section I drilled an entrance hole (diameter 4.5 cm, approxi-

mately the size of the entrance hole drilled by a Downy Woodpecker, *Picoides pubescens*) and deposited three fresh quail eggs. Twenty-two artificial cavity nests were nailed onto the trunks of dead or dying trees, 1–2 m above ground, at 25-m intervals in a 4.2-ha suburban woodlot (J). In the same woodlot I placed 20 open-cup nests alternately on the ground and 1–2 m above ground. Both types of nests were left up for 7 d, at which time they were checked for evidence of predation.

#### RESULTS

In neither of the two largest tracts was there a significant difference in predation rate between the two transect lines (Fisher Exact Probability tests: tract A,  $P > .50$ ; tract B,  $P > .16$ ). Results from the two transects were combined to obtain a single predation value for each tract. In no case did the predation rate in a tract differ significantly between replicates ( $\chi^2$  contingency tests: tract B,  $\chi^2 = 0.46$ ,  $P > .30$ ; tract G,  $\chi^2 = 0.10$ ,  $P > .70$ ; tract I,  $\chi^2 = 1.82$ ,  $P > .10$ ; Fisher Exact Probability test: tract J,  $P > .50$ ).

Only 2% of the experimental nests in Great Smoky Mountains National Park suffered predation (Fig. 1); this rate is significantly lower than the predation rate at any other site ( $\chi^2$  Contingency tests: tracts C, E, I, J, K, all  $\chi^2 \gg 10.83$ ,  $P < .001$ ; Fisher Exact Probability tests: tracts B and D,  $P < .05$ , tracts F and H,  $P < .01$ , tract G,  $P < .001$ ). Of the 10 Maryland sites, the largest (905 ha) also had the lowest predation rate (18%). This rate differed significantly from those in five smaller tracts, three of which were suburban woodlots ( $\chi^2$  Contingency tests: tract C,  $\chi^2 = 7.31$ ,  $P < .01$ ; tracts E, I, J, all  $\chi^2 \gg 10.83$ ,  $P < .001$ ; Fisher Exact Probability test: tract K,  $P < .001$ ). It did not differ significantly ( $P > .05$ ) from the predation rates in four smaller tracts, three of which were rural woodlots. The pooled predation values for rural and suburban woodlots differed significantly from the 905-ha tract ( $\chi^2 = 9.00$ ,  $P < .01$  for rural woodlots;  $\chi^2 = 26.30$ ,  $P < .001$  for suburban woodlots). Average predation rates were higher in suburban woodlots (47.5%) than in rural woodlots (47.5%).

Predators identified by the track sampling included: dog (tract E), cat (I), raccoon (E, G, I, J), opossum (*Didelphis virginiana*) (J), striped skunk (J), and Blue Jay (G, J, confirmed by direct observation). Since predators often robbed the nests without leaving identifiable tracks, this list cannot be considered complete.

Ground nests were more susceptible to predation than aboveground nests. In none of the 11 sites were aboveground nests preyed upon to a significantly higher degree than ground nests, but a significantly higher proportion of ground nests suffered predation at two sites: tract C ( $\chi^2 = 10.95$ ,  $P < .001$ ) and tract H (Fisher Exact Probability test,  $P < .01$ ).

The comparison of open-cup nests with cavity nests revealed significant differences in their susceptibility to predation. Predation was much greater on open-cup

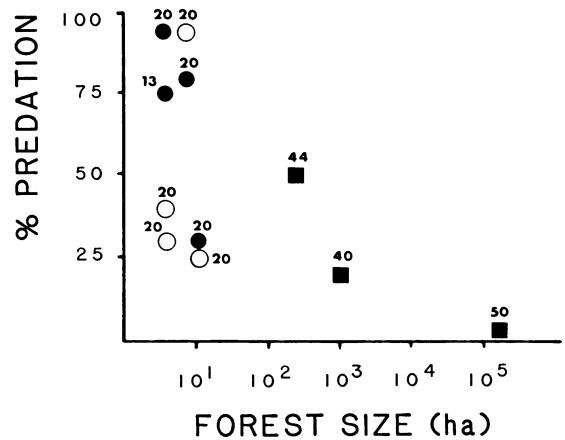


FIG. 1. Percentage of nests preyed upon as a function of forest size. ■ large forest tracts, ○ rural fragments, ● suburban fragments. The number above each point is the number of experimental nests.

nests (95%) than on cavity nests (0%) ( $\chi^2 = 34.43$ ,  $P < .001$ ).

#### DISCUSSION

Several factors may account for the higher rates of predation in small woodlots. Numbers of some nest predators, such as the Blue Jay and American Crow, have increased in recent years as a result of man-induced changes in the landscape (Bock and Lepthien 1976; D. Bystrak, *personal communication* of data from the United States Fish and Wildlife Service Breeding Bird Survey). Small woodlots support few, if any, large predators like mountain lion, bobcat, and large hawks and owls that may regulate populations of smaller nest predators (Matthiae and Stearns 1981, Whitcomb et al. 1981). Finally, three avian nest predators (Blue Jay, American Crow, and Common Grackle, *Quiscalus quiscula*) are more common along forest edges than in the forest interior (Robbins 1980, Whitcomb et al. 1981; D. Wilcove, *personal observation*). Small woodlots may thus have higher densities of these species than large tracts.

Of the three large tracts, Great Smoky Mountains National Park is the most nearly pristine. Its comparatively low rate of nest predation presumably resembles that under which the forest songbirds evolved. Today not even the largest Maryland tract approaches the 2% predation rate found in the Smoky Mountains.

The high predation rate (48%) in the 283-ha site may reflect the fact that this tract was a long, narrow corridor of forest along the Patuxent River, and therefore easily penetrated by nest predators from adjacent habitats. The other tracts were more nearly circular in shape. This 283-ha strip was, however, adjacent to extensive forest, perhaps accounting for the continued presence of neotropical migrants.

The generally higher predation rates in suburban as opposed to rural woodlots are probably due to higher

densities of nest predators in the suburban tracts, since at least four nest predators reach their highest densities in suburban environments. These include the Blue Jay (Fretwell 1972), Common Grackle (Robbins 1980), gray squirrel (Flyger 1970), and raccoon (Hoffman and Gottschang 1977). Dogs, cats, and rats are also probably more numerous in woodlots near human dwellings than in isolated rural woodlots.

Aspects of the breeding biology of the neotropical migrants make them especially vulnerable to nest loss (Robbins 1980, Whitcomb et al. 1981). Four of the species most sensitive to forest fragmentation in Maryland (Black-and-white Warbler, Worm-eating Warbler, Ovenbird, Hooded Warbler) nest on or near the ground, while most forest-dwelling residents and short-distance migrants nest 2 m or more above the ground (Robbins 1980, Whitcomb et al. 1981). In some woodlots, at least, nesting near the ground means an increased risk of predation. Most neotropical migrants construct open, cup-like nests. In central Maryland, nonmigratory woodpeckers, chickadees, and nuthatches nest in tree cavities, but only one forest-dwelling neotropical migrant (Great Crested Flycatcher, *Myiarchus crinitus*) does so. Cavity nests are thought to be less vulnerable to predators than open-cup nests (Alerstam and Hogstedt 1981, Whitcomb et al. 1981). This idea was strongly supported by my cavity vs. open-cup nest experiment in the suburban woodlot. It is not surprising, then, that many of these cavity-nesting birds commonly occur in small woodlots (Whitcomb et al. 1981), including forests with high experimental predation rates (D. Wilcove, *personal observation*).

Forest fragmentation is associated with a number of changes that are harmful to populations of neotropical migrants. These include cowbird parasitism, the loss of habitat heterogeneity, potential barriers to dispersal between woodlots, and increased nest predation. The extent to which any one of these factors has harmed songbird populations is unknown. Nonetheless, if nest predation acts in concert with the other factors, then a relatively small increase in nest predation could cause extinctions. Population declines may also be hastened by the tendency for unsuccessful breeders to disperse from the site of a failed nesting attempt (Harvey et al. 1979, Greenwood 1980).

The failure of small woodlots to retain populations of neotropical migrants has been well documented. However, the survival of these birds in much larger tracts should not be taken for granted. Given the higher rates of nest predation in the largest Maryland sites compared to the Smoky Mountains, it is possible that forest tracts of 900 or more hectares may eventually experience declines in breeding populations of migratory songbirds.

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