

LACK OF EDGE EFFECT IN NESTING SUCCESS OF BREEDING BIRDS IN MANAGED FOREST LANDSCAPES

ILPO K. HANSKI,¹ TIMOTHY J. FENSKE, AND GERALD J. NIEMI

5013 Miller Trunk Highway, Natural Resources Research Institute,
University of Minnesota, Duluth, Minnesota 55811, USA

ABSTRACT.—We assessed avian nesting success in two forested landscapes (Chippewa and Superior National Forests) in northern Minnesota. We found 311 nests of 33 species in the Chippewa study area and 36 nests of 13 species in the Superior study area. Each nest was classified into one of three general habitat types: open (clearcuts with vegetation <2 m high), regenerating aspen (2–8 m high), or forested (trees >8 m high). Mayfield nesting success for the most common species in the Chippewa (all of which had open-cup nests) averaged 0.43. Nesting success ranged from 0.18 for the Red-eyed Vireo (*Vireo olivaceus*) to 0.76 for the Yellow Warbler (*Dendroica petechia*). Nest predation was the most common mortality factor, causing 89.2% of known failures. Nest predation among ground-nesting birds was significantly higher in the Chippewa (55%) than in the Superior (15%) study area ($P = 0.038$). Nest predation was highest ($P = 0.015$) in the forest (62.2%) and lowest in open (42.2%) and regenerating (47.4%) habitat types. Only canopy cover explained differences in nesting success, which was higher in more open canopies. Distance to forest edge, nest height, and nest concealment had no effect on nesting success in both forested and open habitats. Brown-headed Cowbird (*Molothrus ater*) parasitism was low (9.6% in the Chippewa study area), and parasitized nests were relatively unsuccessful (only 1.7% yielded cowbird fledglings). Neither cowbirds nor nest parasitism was observed in the Superior study area. Received 30 May 1995, accepted 20 August 1995.

CONCERN ABOUT THE DECLINE of forest songbirds during past decades has stimulated many studies to unravel the factors causing the decline (e.g. Whitcomb et al. 1981, Brittingham and Temple 1983, Wilcove 1985, Askins et al. 1990, Rappole and McDonald 1994). Habitat fragmentation, both on the breeding grounds and in Neotropical wintering areas, is purported to affect breeding productivity and survival, therefore influencing bird populations. The spread of human settlement and the increase in agricultural land continue to be important factors causing forest fragmentation and loss of forest area. However, forest management also has a major influence on landscape patterns. Intensive forestry has created mosaics of mature stands mixed with successional stands of various ages. This has increased the amount of edge among stands.

Nest predation is the most important factor causing nesting failures and, thus, reduction in the production of young (e.g. Ricklefs 1969, Martin 1993). Numerous studies on natural and artificial nests have shown that forest fragmen-

tation increases nest predation and reduces breeding success (e.g. Wilcove 1985, Small and Hunter 1988). Fragmentation increases the amount of edge, and nests located near the forest edge may suffer higher predation than nests in the forest interior (see Paton 1994). However, an edge effect has not been found in all studies (e.g. Ratti and Reese 1988, Storch 1991, Berg et al. 1992, Nour et al. 1993, Rudnický and Hunter 1993).

Most of the studies on nesting success in relation to fragmentation have been done in forests within agricultural landscapes (Paton 1994). Increased predation near the edges of fields and grasslands has been explained by a higher density of generalist predators that are able to penetrate the forest and prey on nests. In addition, some predator species may concentrate their nesting and prey searching at forest edges (Andrén 1992, Nour et al. 1993). In contrast, studies of nesting success in forests fragmented by clearcuts, or in young regenerating forests, are few (but see Chasko and Gates 1982, Yahner and Wright 1985, Small and Hunter 1988, Storch 1991, Yahner 1991, Rudnický and Hunter 1993). Furthermore, only a few studies support the hypothesis that nest predation within forested landscapes is higher near the forest edge (Chas-

¹ Present address: Department of Ecology and Systematics, University of Helsinki, P.O. Box 17, FIN-00014, Finland. E-mail: ilpo.hanski@helsinki.fi

ko and Gates 1982, Small and Hunter 1988). Most studies in forested habitats have found no edge effect (Boag et al. 1984, Yahner and Wright 1985, Yahner 1991, Rudnicki and Hunter 1993). Indeed, Storch (1991) found that artificial nests survived better near edges than in the forest interior.

Here, we report results on nesting success of forest birds at two sites in northern Minnesota. Our objectives were to: (1) assess nesting success of the most common forest songbirds, and (2) determine the effect of forest fragmentation and nest-site location on nesting success.

METHODS

We selected two study plots of about 60 ha each for nest searching. One was in the Chippewa National Forest (hereafter "Chippewa," 46°55' N, 94°30' W) and the other in the Superior National Forest ("Superior," 47°45' N, 91°20' W) in north-central and northeastern Minnesota, respectively. Each plot was located within a larger 2.56-km² area in which birds were censused. Forests in both study plots are managed by the U.S. Forest Service.

The Chippewa plot was dominated by various age classes of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) cover types. Age classes were divided into forest (trees >8 m high), regenerating aspen (2–8 m high), and open (recent clearcuts with trees ≤2 m high). Other hardwood species included red maple (*Acer rubrum*), basswood (*Tilia americana*), and red oak (*Quercus rubra*). Deciduous and mixed deciduous-coniferous forests surrounded the plot; the closest agricultural field was approximately 3 km from the plot.

In the Superior plot, the common cover types were aspen and aspen-jack pine (*Pinus banksiana*) forests. This study plot included one clearcut and a stand of red pine (*P. resinosa*) saplings. Deciduous forest, mixed deciduous and coniferous forest, and coniferous forest were typical of the area surrounding the plot. The closest agricultural land was >10 km from the plot.

Two to four people searched for nests daily in both study sites from mid-May until the end of July 1994. Plots were marked with parallel lines of flagging spaced 100 m apart and with coordinates to help locate nests. The location of each nest was marked with a flag that was usually placed at least 10 m from the nest. Nests were checked every three to four days until just before fledging, when they were checked every day. When checking nests, we strived to avoid damaging vegetation and making trails near nests. Nests that fledged at least one young were considered successful. Nests that were too high above ground to be checked directly were considered successful if the parents were seen feeding nestlings and if they at-

tended the nest long enough to cover the incubation and nestling periods typical for the species. When calculating success rates, failures of high nests that we were not able to check were classified as depredated, although these "failures" may have included a few deserted nests. Nests that were found outside the 60-ha searching plots (15% in the Chippewa) were included in the analyses.

We measured nest height and vegetation at each nest in July. Vegetation measurements included total canopy cover, nest cover 1 m above the nest, and nest cover on each of four sides of the nest. By necessity, measurements of vegetation cover were estimated for high nests. When measuring variables of nest location, we followed the guidelines for the minimum nesting productivity variables of the Breeding Biology Research and Monitoring Database (BBIRD; Anonymous 1994). After the breeding season, the location of each nest was determined with a global positioning system and entered into a geographic information system database.

We analyzed the Chippewa data in more detail than the Superior data. We defined edges by the contrasts between the three forest age classes (forest, regenerating, and open). Besides clearcuts and young aspen stands, the open area included a powerline right-of-way and small bogs. We calculated the distance from each nest to the two nearest edge types. The open, regenerating, and forest cover types comprised 33%, 14%, and 53% of the area where the nests were found, respectively.

We calculated three logistic regression models to evaluate nesting success: (1) using all nests combined; (2) using all nests in open areas; and (3) using all nests in forests. The models were calculated with forward, backward, stepwise, and score methods to achieve the best model (SAS Institute 1990). All the methods yielded similar results. The variables included in the models were total canopy cover; vegetation cover 1 m above the nest; mean cover on each of four sides of the nest; nest height; area of habitat stand where a nest was located; distance to the nearest edge; and distances to open areas, regenerating aspen, and forest edge. Only bird species that build an open-cup nest were included in the analyses. The number of nests from regenerating aspen stands was too low ($n = 19$) for a separate analysis. Nesting success was estimated using the Mayfield method (Mayfield 1961, 1975) for species with a sample size of 10 or more nests.

To evaluate whether the relationship between nesting success and distance to open edge was independent of bird species, log-linear models were fitted to three-way contingency tables using data from the three most abundant species nesting in the forest cover type. Nests were divided into contingency classes as follows: (1) bird species (Least Flycatcher [*Empidonax minimus*], Red-eyed Vireo [*Vireo olivaceus*], and American Redstart [*Setophaga ruticilla*]); (2) nest fate (suc-

TABLE 1. Fate of nests found in the Chippewa National Forest study plot in 1994.

Species	n	Fate of nest			Unknown	Proportion that failed ^b	Cowbird parasitism ^c	Nesting success ^d
		Successful	Failed ^a	Unknown				
Ruffed Grouse (<i>Bonasa umbellus</i>)	1	1	—	—	0.00	—	—	
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	2	1	1	—	0.50	—	—	
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	8	7	1	—	0.13	—	—	
Hairy Woodpecker (<i>Picoides villosus</i>)	2	—	2	—	1.00	—	—	
Eastern Wood-Pewee (<i>Contopus virens</i>)	4	4	—	—	0.00	—	—	
Alder Flycatcher (<i>Empidonax alnorum</i>)	2	1	1	—	0.50	—	—	
Least Flycatcher (<i>E. minimus</i>)	48	6	39	3	0.87	—	0.24	
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	1	—	—	1	—	—	—	
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	2	2	—	—	0.00	—	—	
Tree Swallow (<i>Tachycineta bicolor</i>)	4	—	—	4	—	—	—	
Blue Jay (<i>Cyanocitta cristata</i>)	3	2	1	—	0.33	—	—	
Black-capped Chickadee (<i>Parus atricapillus</i>)	1	—	1	—	1.00	—	—	
Veery (<i>Catharus fuscescens</i>)	11	5	6	—	0.55	—	0.56	
American Robin (<i>Turdus migratorius</i>)	3	2	1	—	0.33	—	—	
Gray Catbird (<i>Dumetella carolinensis</i>)	10	3	7	—	0.70	—	—	
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	23	6	15	2	0.71	—	0.42	
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	1	—	1	—	—	—	—	
Red-eyed Vireo (<i>V. olivaceus</i>)	59	10	43	6	0.81	8	0.18	
Golden-winged Warbler (<i>Vermivora chrysoptera</i>)	3	1	2	—	0.67	—	—	
Yellow Warbler (<i>Dendroica petechia</i>)	18	14	4	—	0.22	1	0.76	
Chestnut-sided Warbler (<i>D. pensylvanica</i>)	16	10	6	—	0.38	3 (2)	0.59	
American Redstart (<i>Setophaga ruticilla</i>)	29	16	12	1	0.43	—	0.54	
Ovenbird (<i>Seiurus aurocapillus</i>)	11	4	7	—	0.64	—	0.48	
Common Yellowthroat (<i>Geothlypis trichas</i>)	7	2	5	—	0.71	2 (1)	—	
Scarlet Tanager (<i>Piranga olivacea</i>)	7	4	2	1	0.33	—	—	
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	13	5	8	—	0.62	—	0.32	
Indigo Bunting (<i>Passerina cyanea</i>)	3	1	2	—	0.67	1	—	
Chipping Sparrow (<i>Spizella passerina</i>)	1	1	—	—	0.00	—	—	
Clay-colored Sparrow (<i>S. pallida</i>)	1	1	—	—	0.00	—	—	
Song Sparrow (<i>Melospiza melodia</i>)	10	6	4	—	0.40	1	0.24	
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	2	—	—	2	—	—	—	
Purple Finch (<i>Carpodacus purpureus</i>)	4	2	2	—	0.50	1	—	
American Goldfinch (<i>Carduelis tristis</i>)	1	—	—	1	—	—	—	
Total or mean	311	117	173	21	0.54	17 (3)	0.43	

^a Includes deserted nests.^b Includes nests that were definitely preyed upon and nests that were probably (high and cavity nests) preyed upon. Nests of unknown fate omitted. Species with $n > 5$ used to calculate the mean.^c Number of nests parasitized by cowbirds, with number of nests fledging cowbirds in parentheses.^d Proportion of attempts successful estimated by the Mayfield (1961) method.

TABLE 2. Fate of nests found in the Superior National Forest study plot in 1994. See Table 1 for definitions of column headings.

Species	n	Fate of nest			Proportion that failed
		Successful	Failed	Unknown	
American Woodcock (<i>Scolopax minor</i>)	1	1	—	—	0.00
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	1	—	—	1	—
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	1	1	—	—	0.00
Brown Creeper (<i>Certhia americana</i>)	1	1	—	—	0.00
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	1	1	—	—	0.00
Hermit Thrush (<i>Catharus guttatus</i>)	3	1	1	1	0.50
Red-eyed Vireo (<i>Vireo olivaceus</i>)	2	2	—	—	0.00
Nashville Warbler (<i>Vermivora ruficapilla</i>)	2	2	—	—	0.00
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	9	4	5	—	0.56
Ovenbird (<i>Seiurus aurocapillus</i>)	5	5	—	—	0.00
Chipping Sparrow (<i>Spizella passerina</i>)	5	4	1	—	0.20
Song Sparrow (<i>Melospiza melodia</i>)	2	1	1	—	0.50
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	3	1	1	1	0.50
Total or mean	36	24	9	3	0.25

successful or failed); and (3) distance to open edge (0 to 25 m, >25 to 50 m, and >50 m). Nests of Least Flycatchers, Red-eyed Vireos, and American Redstarts constituted 69.3% of all nests found in the forest cover type.

RESULTS

We found and monitored 311 nests in the Chippewa (33 species) and 36 nests in the Superior (13 species) study plots (Tables 1 and 2). Nests abandoned before egg laying were excluded from analyses. In the Chippewa plot, nests of the 10 most common species (Least Flycatcher, Veery [*Catharus fuscescens*], Cedar Waxwing [*Bombycilla cedrorum*], Red-eyed Vireo, Chestnut-sided Warbler [*Dendroica pensylvanica*], Yellow Warbler [*D. petechia*], Ovenbird [*Seiurus aurocapillus*], American Redstart, Rose-breasted Grosbeak [*Pheucticus ludovicianus*], and Song Sparrow [*Melospiza melodia*]) comprised 75% of all nests found. Nesting success was low in the Chippewa plot, averaging 0.43 for the 10 most common species (all open-cup nesters; Table 1). Nesting success varied among individual species, with the lowest values for Red-eyed Vireos (0.18), Least Flycatchers (0.24), and Song Sparrows (0.24) and the highest for Chestnut-sided Warblers (0.59) and Yellow Warblers (0.76). For several species (i.e. Veery, Ovenbird, and Song Sparrow), sample sizes may have been too small to calculate reliable Mayfield estimates. In the Superior plot, sample sizes for all species were too small to calculate Mayfield estimates.

Nest predation was the most common cause of nesting failures, accounting for 89.2% of all known failures (both study sites combined, $n = 102$). The remaining nest failures were classified as deserted, mostly when we found cold eggs or dead nestlings in the nest.

We compared predation of ground nests that were found during building or incubation between the Chippewa and Superior plots (deserted nests omitted). Nest predation (i.e. percent of nests depredated) for ground nests was significantly higher at Chippewa (55%, $n = 29$) than at Superior (15%, $n = 13$; χ^2 with Yates correction = 4.29, $df = 1$, $P = 0.038$). Nest-predation data in three distance categories from the forest edge and in three height classes are presented for the Chippewa study plot in Table 3. Nest predation differed significantly among the three habitat classes ($\chi^2 = 8.44$, $df = 2$, $P = 0.015$; Fig. 1), being lowest in open areas (42.2%) and regenerating stands (47.4%) and highest in forests (62.2%). If abandoned nests are included in the analysis, the difference is still significant ($\chi^2 = 7.38$, $df = 2$, $P = 0.025$).

Based on logistic regression, only one variable, total canopy cover, was significant in explaining nesting success for all nests ($\chi^2 = 12.59$, $df = 1$, $P = 0.004$). The parameter estimate was negative, indicating that nests located in sites with high canopy cover were less successful than those in sites with low cover. In the open area and forest, no models were significant. Thus, none of the characteristics of the nest site (e.g. nest height, nest concealment, or nest lo-

TABLE 3. Nest predation relative to habitat type, nest height, and distance from open edge (forest nests) and from forest edge (open habitat nests) in the Chippewa National Forest, 1994.

	<i>n</i>	Percent of nests depredated
Open		
Total	83	42.2
Nest height (m)		
0 to 0.3	17	47.1
>0.3 to 2.0	59	40.7
>2.0	7	42.9
Distance from edge (m)		
0 to 25	37	43.2
>25 to 50	23	39.1
>50	23	43.5
Regenerating aspen		
Total	19	47.4
Forest		
Total	127	62.2
Nest height (m)		
0 to 0.3	12	41.7
>0.3 to 2.0	43	62.8
>2.0	72	65.3
Distance from edge (m)		
0 to 25	36	58.3
>25 to 50	51	66.7
>50	40	60.0

cation in relation to edge) explained nesting success. The result for all nests can be explained by the higher success at nests in open areas with little canopy cover (Fig. 1), especially because canopy cover was not significant in the models calculated separately for open and forest cover types.

Using data from three most common species in the forest cover type (i.e. Least Flycatcher, Red-eyed Vireo, and American Redstart), the best log-linear model obtained (see Toft 1984) indicated that nest fate was dependent on bird species, but that neither nest fate nor the interaction (bird species and nest fate) was dependent on distance to the nearest open edge ($G = 13.30$, $df = 12$, $P = 0.38$).

Brown-headed Cowbirds (*Molothrus ater*) parasitized only 17 of 178 nests (9.6%) in the Chippewa study plot (Table 1). Three of these nests (1.7%) yielded cowbird fledglings. Parasitism by Brown-headed Cowbirds probably caused four nest desertions in the egg-laying and incuba-

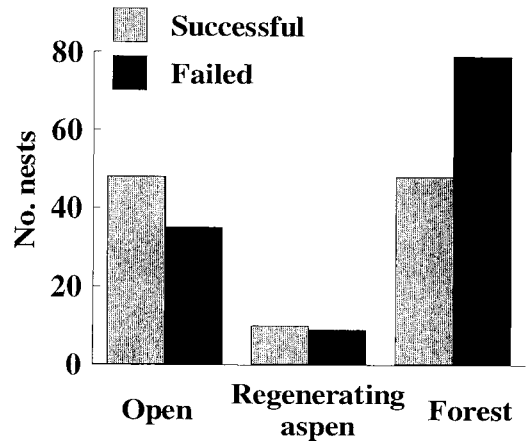


FIG. 1. Number of successful and depredated nests in three cover types. Only open-cup nests included.

tion stages, including desertions at three Red-eyed Vireo nests and one Yellow Warbler nest. Neither parasitized nests nor adult Brown-headed Cowbirds were observed in the Superior study plot.

DISCUSSION

Nesting failure of open-cup-nesting birds was high, especially in the Chippewa study plot. There seemed to be regional differences in nesting success, but the data from the Superior plot are too few to draw definitive conclusions. Nest predation was the most common factor causing failure, as has been found in several other studies (e.g. Ricklefs 1969, Martin 1993). The mean nesting success of the 10 most common species was 43%, which is similar to the success rate that Martin (1992) reported in open-nesting Neotropical migrants (i.e. 39%). However, success rates varied widely among species, from a low of 18% in the Red-eyed Vireo to a high of 76% in the Yellow Warbler.

Absence of edge effects.—In both forest and open habitats, we found no evidence that nesting success was influenced by proximity to the edge. This result can be interpreted in at least three ways. First, edges may indeed have no effect on nest predation at the Chippewa study site. Second, the forests at Chippewa may be comprised of relatively small patches so that few areas can be designated as interior or nonedge habitat. In essence, the effect of the edge may extend to all parts of the forest. Third, because our study was

conducted for only one year, the results may not be representative of the long-term average.

The results of other studies in forested landscapes generally support the first explanation; i.e., no edge effect was detected (see Introduction). Furthermore, the effect of the edge seems to extend up to 50 m into the forest (see Paton 1994). In our study, 31% of the forest nests were located more than 50 m from the edge, but predation was not lower at these nests.

Nest predator behavior and forested landscapes.—Most studies on nesting success in relation to edge and forests have occurred in landscapes fragmented by agriculture (see Paton 1994). Cutting forests for agricultural land has created permanent open areas that are favored by predators of open nests such as striped skunks (*Mephitis mephitis*) and species of the family Corvidae (Andrén 1992, Picman and Schriml 1994). The increased nest predation at the forest edges is caused by a combination of forest-dwelling predator species and open-habitat species that are able to penetrate the edges of forests. In contrast, Rudnický and Hunter (1993) emphasized that edge types and the density and species composition of predator assemblages in forested landscapes often differ from those found in agricultural landscapes. Therefore, higher nest predation near edges may not be a general rule for all habitats (Berg et al. 1992). This idea receives support from most of the nest-productivity studies that have been conducted in forested landscapes (see above) and from the fact that predator assemblages differ among different habitats (Picman and Schriml 1994).

Following timber harvest, landscapes often go through a short-lived open stage, which is rapidly followed by succession and later canopy closure. The open stage may be too brief to permit grassland nest predators to colonize the harvested area. It also is unlikely that there are any species of nest predators that are specialized for living in clearcuts. In contrast, there may be forest-inhabiting predators that forage in edges, and they may benefit from edges created by forest cutting. This could increase the overall predator density at edges.

Natural regeneration of forests following disturbance may have been sufficient to allow the evolution of edge preferences for some predator species. Natural forests are characterized by disturbances such as forest fires and wind blow-downs, which create a mosaic of open, early

successional, and mature forest types (e.g. Zackrisson 1977, Heinselman 1981). Forest cutting may partly imitate natural disturbances by creating young successional stages. However, the structure of successional stages following natural disturbances and that following forest management differ from each other in many important ways (Pastor and Mladenoff 1992, Syrjänen et al. 1994, Hutto 1995).

Nest predators and nest habitat.—Nest predation was lower in open habitats than in forests. This result supports the idea that there are fewer predators in clearcut areas and possibly fewer, if any, specialist predators in clearcuts and young successional stands. A similar pattern was found by Yahner and Wright (1985) and Seitz and Zegers (1993).

Besides the location of nests within the forest or their position in relation to edges, other factors may affect nest survival. The selected nest site, its concealment, or its height may affect the vulnerability of the nest to predation (e.g. Martin 1992 and references therein). Many studies have found that well-concealed nests are less vulnerable to predation than are more exposed open nests (see Martin 1992), but we did not find this. A plausible explanation is that nest concealment has a minor effect on vulnerability to predation, especially if the main predators are mammals that use olfactory cues to locate nests (see below).

Nest height and nest predation also were not related. Several authors have found differences in nest predation among ground, shrub, and tree nests, but no general trend exists (Ricklefs 1969; Nilsson 1984; Martin 1992, 1993). Apparently, more important than nest height per se are the density and local structure of the predator assemblage. This notion is supported by the results of some nest-predation experiments with artificial nests. Nest predation differed between sites (even though habitats were similar) because the spatial distribution of predators differed (e.g. Reitsma et al. 1990, Leimgruber et al. 1994, Fenske 1995).

Potential nest predators.—Adjacent to the Chippewa plot, we placed two automatic cameras near artificial ground nests to identify species preying on nests (Fenske 1995). Eight species of mammals were recorded preying on Northern Bobwhite (*Colinus virginianus*) eggs in the nests: fisher (*Mustela pennanti*; 8 cases), eastern chipmunk (*Tamias striatus*; 5), red-backed

vole (*Clethrionomys gapperi*; 4), deer mouse (*Peromyscus maniculatus*; 3), red squirrel (*Tamiasciurus hudsonicus*; 3), black bear (*Ursus americanus*; 2), gray squirrel (*Sciurus carolinensis*; 1), and striped skunk (1). In addition, a flying squirrel (*Glaucomys* sp.) was observed once at a nest, but it did not eat eggs. No avian predators were identified with the cameras, but Blue Jays (*Cyanocitta cristata*) were nesting and commonly seen in our study plot. These results indicate that mammalian predators were responsible for most nest losses on the forest floor. Because birds use other cues besides olfaction for finding nests (e.g. behavior of adults near the nest), they may prey on active nests on the ground. Although only ground nests were monitored with cameras, the local abundance of chipmunks and tree squirrels may partially explain the high frequency of nest predation observed in tree-nesting species like the Least Flycatcher and Red-eyed Vireo.

Brown-headed Cowbirds.—Nest parasitism seemed to have a minor effect on the nesting success in the Chippewa study plot and probably no effect in the Superior plot during our study. Brown-headed Cowbirds often parasitize open nests in agricultural landscapes (Brittingham and Temple 1983). Cowbirds forage on agricultural land, lawns, and bare ground and can parasitize nests up to 6.7 km from their foraging areas (Rothstein et al. 1984). At our study plots, most open areas created by forest management do not provide appropriate foraging habitat for cowbirds and, generally, do not support large numbers of cowbirds. The nearest fields and pastures were only 3 km from the Chippewa plot, which is well within the foraging range documented for Brown-headed Cowbirds. The consequences of parasitism to nesting success may be overestimated if one looks at the parasitism rate alone (Martin 1992). This is because, as we found, most of the parasitized nests were lost to nest predators (see Table 1).

Conclusions.—The results of our study support many of the earlier findings that the proximity of nests to the edge has no effect on nesting success for birds with open-cup nests in forested landscapes. Studies on natural nests are relatively scarce, and more studies are needed, especially in different forest types and in landscapes that are changed through forestry practices. To adequately evaluate the factors that affect nest productivity in forest birds, more

nesting studies need to be coupled with data on local predator assemblages, especially data on predator densities, searching tactics, spacing behavior, and densities of alternate prey.

ACKNOWLEDGMENTS

We thank our field assistants E. Engstrom, R. Finder, P. Larson, and R. Van Horne for their efforts in searching and monitoring nests. P. Polzer and M. White completed the data organization and compilation of maps for the GIS analyses. A. Lima calculated Mayfield estimates and performed statistical analyses. Funding for the project was appropriated by the Minnesota State Legislature from the Environmental Trust Fund as recommended by the Legislative Commission on Minnesota Resources. We appreciate the helpful comments on this manuscript from J. Green, R. S. Greenberg, J. Hanowski, L. Pfannmuller, and J. H. Rappole.

LITERATURE CITED

- ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* 73:794–804.
- ANONYMOUS. 1994. BBIRD field protocol. Breeding biology research and monitoring database. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7:1–57.
- BERG, Å., S. G. NILSSON, AND U. BOSTRÖM. 1992. Predation on artificial wader nests on large and small bogs along a south-north gradient. *Ornis Scandinavica* 23:13–16.
- BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER. 1984. Egg loss among Spruce Grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62:1034–1037.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- CHASKO, G. G., AND J. E. GATES. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* No. 82.
- FENSKE, T. J. 1995. Predation of artificial ground nests at two types of edges in a forest-dominated landscape. M.S. thesis, University of Minnesota, Duluth.
- HEINSELMAN, M. L. 1981. Fire and succession in the conifer forest of northern North America. Pages 374–405 in *Forest succession: Concepts and applications* (D. C. West, H. H. Shugart, and D. B. Botkin, Eds.). Springer-Verlag, New York.
- HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in northern

- Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9:1041-1058.
- LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58:254-260.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455-471 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D. C.
- MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: Revising the dogmas. *American Naturalist* 141:897-913.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scandinavica* 15:167-175.
- NOUR, N., E. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: Different trends in birds and mammal predators. *Ecography* 16:111-116.
- PASTOR, J., AND D. J. MLADENOFF. 1992. The southern boreal-northern hardwood forest border. Pages 216-240 in *A systems analysis of the global boreal forest* (H. H. Shugart, R. Leemans, and G. B. Bonan, Eds.). Cambridge University Press, Cambridge.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17-26.
- PICMAN, J., AND L. M. SCHRIML. 1994. A case study of temporal patterns of nest predation in different habitats. *Wilson Bulletin* 106:456-465.
- RAPPOLE, J. H., AND M. V. McDONALD. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652-660.
- RATTL, J. T., AND K. P. REESE. 1988. Preliminary test of the ecological trap hypothesis. *Journal of Wildlife Management* 52:484-491.
- 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* No. 9.
- ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. *Ecology* 65:77-88.
- RUDNICKY, T. C., AND M. L. HUNTER, JR. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358-364.
- SAS INSTITUTE INC., 1990. SAS technical report P-200, SAS/STAT software: CALIS and LOGISTIC procedures, release 6.04. Cary, North Carolina.
- SEITZ, L. C., AND D. A. ZEGERS. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. *Condor* 95:297-304.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62-64.
- STORCH, I. 1991. Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie. *Ornis Scandinavica* 22:213-217.
- SYRJÄNEN, K., R. KALLIOLA, A. PUOLASMAA, AND J. MATTSSON. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Annales Zoologici Fennici* 31:19-34.
- TOFT, C. A. 1984. Resource shifts in bee flies (Bombyliidae): Interactions among species determine choice of resources. *Oikos* 43:104-112.
- 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 the eastern deciduous forest. Pages 125-205 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- YAHNER, R. H. 1991. Avian nesting ecology in small even-aged aspen stands. *Journal of Wildlife Management* 55:155-159.
- YAHNER, R. H., AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: Effect of edge and plot age. *Journal of Wildlife Management* 49:508-513.
- ZACKRISSON, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29:22-32.