

**RELATIONSHIPS BETWEEN MULTI-SCALE HABITAT FEATURES
AND BREEDING BIOLOGY OF OVENBIRDS AND HERMIT THRUSHES**

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CHAPTER 1: RELATIONSHIPS BETWEEN MULTI-SCALE HABITAT FEATURES AND BREEDING BIOLOGY OF GROUND- NESTING FOREST SONGBIRDS

ABSTRACT.-Many Neotropical migratory songbirds breeding in temperate forests have declined across their geographic ranges. Populations breeding in large, contiguous forests like those in boreal and northern hardwood forests may support populations breeding in fragmented hardwood forests of the central United States. If this is correct, then regional declines may exacerbate continental declines. In northern Minnesota and northern Wisconsin, northern hardwoods are being modified by silvicultural, agricultural and other anthropogenic practices. These changes may explain recent rises in nest predators that favor human-dominated landscapes and regional declines in several ground-nesting songbirds. To address this problem, I assessed effects of habitat characteristics at multiple scales on the breeding biology of two ground-nesting songbirds in mature northern hardwood stands. During summer of 2000, I located and monitored 88 ground nests of songbirds in Aitkin County, Minnesota. In addition, I tracked 219 Ovenbird (*Seiurus aurocapillus*) territories to determine densities, pairing success, and fledging success. At the microsite scale, only fern cover consistently predicted nest predation for both all ground nesters and Ovenbirds. A substrate with shallow leaf litter and few ferns surrounded by a microsite with higher fern cover was associated with depredated Ovenbird nests. At the patch scale, Ovenbird nest predation was higher away from clearcuts. Using different radii around plot centers, both ground nest survival rates and Ovenbird fecundity 1) increased as forest patch size increased within 3-3.5 km, and 2) decreased as forest edge increased within 1.25-1.5 km. No particular edge type within 1.25 km of plot centers could explain the variation in nesting success or fecundity. Based on these results, I suggest that ground nest predation may be high in areas with shallow leaf litter, high fern cover, small forest patches, and high forest edge density. Evaluating how nesting success varies with habitat characteristics at multiple scales is critical for assessing potential effects of forest management on songbirds in northern hardwoods.

INTRODUCTION

MOST INSECTIVOROUS SONGBIRD SPECIES that breed in forests of eastern North America and winter in southern latitudes have experienced declines (Robbins et al. 1989, Böhning-Gaese et al. 1993). Several causes for the declines have been proposed, but elevated nest predation on breeding grounds is among the primary causes (Böhning-Gaese et al. 1993). It has been proposed that populations breeding in large, contiguous forests of northern Minnesota and northern Wisconsin support populations breeding in fragmented oak-hickory forests of the midwestern United States (Robinson et al. 1995). If this theory is correct, then a regional decline in songbird populations that breed in northern areas may exacerbate continental declines.

In northern Minnesota and northern Wisconsin, contiguous forest tracts are being increasingly reduced by silvicultural practices which favor early-successional species (Hanowski 1999). These alterations and increasing temperatures related to climate change may relate to the recent regional rise in populations of mammals that favor edges (Berg 1999). Concurrently, the majority of declining bird species in this region were ground-nesting songbirds (Lind et al. 2001). A possible mechanism for this decline is elevated nest predation levels by mammals or birds that are attracted to areas perforated by silviculture. It has been reported that nest depredation is the primary cause of nest failure for most open-cup nesting Neotropical migratory songbirds (Martin 1992). Thus, habitat alterations by humans may be driving regional songbird declines.

Habitat features and associated nest predators potentially determine whether young birds fledge from nests. Discovering which scales of habitat are related to nest predation is important for assessing impacts of habitat changes on songbird populations. Spatial scales of habitat include the microsite, patch and landscape. Among the finest levels is

the microsite, which is the immediate area surrounding a nest within a patch. A microsite for a ground nest includes the immediate substrate of the nest and the surrounding cover. A nest built on a unique substrate relative to its microsite may be more conspicuous and thus more vulnerable to predation than a nest in a substrate that matches its microsite (Martin and Roper 1988). This “similar substrate” hypothesis has been tested with shrub-nesting songbirds (Martin and Roper 1988, Kilgo et al. 1996) but not with ground-nesting songbirds.

A forest patch contains many nest microsites and is situated within a forested landscape. Each patch consists of a characteristic type or assemblage of tree species. The prey availability within a patch and predator densities in surrounding patches could interact as important influences on songbird nesting success within a patch. In particular, proximity to silvicultural edges has been shown to have a negative impact on nest predation of ground nests (King et al. 1996, Fenske-Crawford and Niemi 1997, Flaspohler et al. 2001b, Manolis 1999). Not all studies, however, have found this edge effect (e.g., Yahner and Wright 1985). Edges between a forest patch and the surrounding matrix can attract a high diversity of organisms, including nest predators (e.g., Dijak and Thompson 2000). This could lead to decreased breeding productivity in patches adjacent to these edges.

The dispersion, joining, and diversity of individual patches within a landscape (see Wiens et al. 1993) can have an impact on nesting success of songbirds within these patches. Landscape composition can be described both by the configuration of habitat patches and by the total amount of specific habitat types at a given scale. For example, areas with high proportions of forest cover may provide population sources for ground-nesting songbirds, while areas with low amounts may serve as population sinks (Donovan

et al. 1997).

For our purpose, fragmentation is the conversion of a forested landscape from intact tracts to parceled patches separated by alien habitat types (Lord and Norton 1990, Hunter 1996: figure 11) which affects patch configurations. Oftentimes, studies attempting to address effects of fragmentation on nesting success only addressed effects of habitat amount within the landscape and not configuration (e.g., Brittingham and Temple 1983, Yahner and Scott 1988, Robinson et al. 1995, Donovan et al. 1997, Tewksbury et al. 1998, Porneluzi and Faaborg 1999). It has been shown that the amount of edge can be independent of forest cover (Rosenberg et al. 1999, Trzcinski et al. 1999). For instance, a highly fragmented area can have more forest cover than a relatively unfragmented one.

Unlike many forests of the lower midwestern U.S. which are highly fragmented and reduced to low proportion of forest cover, forests of northern Minnesota are generally perforated by wetlands, small farms and silviculture while providing a high proportion of forest cover. Studies investigating the effects of the latter landscape composition on breeding productivity of songbirds are limited (e.g., Tewksbury et al. 1998). In addition, investigations into clearcut edge effects often lack a sufficient sample size of ground nests (e.g., Hanski et al. 1996) even though ground nests may be the most sensitive to clearcut edges (Flaspohler et al. 2001b). Furthermore, most studies have investigated how habitat features influence nest fate at one or two similar spatial scales, while few have considered multiple, disparate scales simultaneously (e.g., Manolis 1999).

These issues are critical gaps in our understanding of songbird nesting ecology. In a response to this knowledge gap, I investigated the relative importance of each scale of habitat features for breeding biology of ground-nesting forest songbirds in mature forests

of east-central Minnesota. Ground cover near the nest, distances to edges and independent effects of forest cover and forest edge were considered as predictive variables for indices of breeding productivity including nesting success and fecundity.

The null hypotheses relating habitat characteristics to breeding success of ground-nesting songbirds were 1) nests built on substrates in microsites containing many potential substrates are equally vulnerable to predation as those built on unique substrates, 2) nests built far from clearcut edges are equally vulnerable to predation as those near clearcuts, and 3) breeding productivity is not related to amount of mature forest cover, mean forest patch size, or edge density. Finally, management suggestions are given that aim to facilitate the maintenance of ground-nesting forest songbird populations.

STUDY AREA AND METHODS

Study site selection.- Before selecting study sites, the following criteria were chosen: 1) upland stands ≥ 50 years of age dominated by sugar maple (*Acer saccharum*), basswood (*Tilia americana*) or red oak (*Quercus rubra*), which I defined as northern hardwoods, to minimize stand-level differences between plots, 3) three stands adjacent to a ≤ 15 year old clearcut, and three ≥ 0.5 km away from such clearcuts to enable comparisons between the two landscape contexts, 4) stands > 10 km apart to minimize spatial autocorrelation and to ensure independent nest predator communities among sites (see Donovan et al. 1997, Fenske-Crawford and Niemi 1997), and 5) stands < 35 km from study headquarters (Rice Lake National Wildlife Refuge in Aitkin County, Minnesota) to ensure logistical efficiency.

I acquired digitized forest stands from the Cooperative Stand Assessment (CSA) protocol (Minnesota Interagency Information Cooperative 2000) and used this as a base

layer from which I selected six mature northern hardwood stands (\bar{x} = 70.0 years, range: [57, 91]). The CSA data were used again to ensure that three of the six stands were adjacent to recent clearcuts (n = 14, \bar{x} = 10.0 years, [0, 14]), and three were at least 0.5 km from recent clearcuts.

Study site description.-Dominant tree species on study plots were sugar maple, basswood and red oak. Paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), black ash (*Fraxinus nigra*) and red maple (*Acer rubra*) were also present in most stands. Understory tree and shrub species included ironwood (*Ostrya virginiana*), beaked hazel (*Corylus cornuta*), leatherwood (*Dirca palustris*), and saplings of dominant canopy species. Herbaceous species included sedges (*Carex* spp.), large-leafed aster (*Aster macrophyllus*), ferns (Pteridaceae) and club mosses (*Lycopodium* spp.).

Landscape metrics.- A 30 x 30 m resolution image with 54 land cover classes based on Landsat imagery (Wolter et al. 1995) was used to obtain landscape metrics. The image was overlaid with a rasterized image of recent clearcuts based on the CSA and then reclassified into two categories: mature forest and cover types other than mature forest (wetlands, brush, natural openings, agriculture, development) (Fig. 1). Three metrics were used to describe the composition and configuration of mature forest surrounding the study plots including percent forest cover, mature forest edge density, and mean mature forest patch size. These measurements were made at 1 km, 1.25 km, 1.5 km, 2 km, 2.5 km, 3 km and 3.5 km radii centered on plot centroids. The range of buffer widths was chosen to cover each plot entirely and to avoid overlap between plots. The width intervals were chosen to test for landscape-scale effects within that range.

Raw landscape metrics were obtained using the AREA and PERIMETER modules in the computer program Idrisi32 (Appendix 4; Clark Labs 1999). The goal of the

landscape analysis was to use a small number of landscape variables to conduct an exploratory investigation rather than a formal test of a hypothesis. Percent forest cover was calculated as the percentage of pixels coded as mature forest. Edge density was defined as the total amount of mature forest edge per unit area. To obtain the actual amount of edge between cover types, the circular perimeter of the buffer itself was subtracted from the total perimeter of pixels within the buffer. Mean patch size was calculated by dividing the total mature forest area by the number of mature forest patches.

The original image consisted of only two different cover types (mature forest and other), and therefore effects by differing edge types were ignored in the initial analyses. To investigate effects of different types of edges on reproductive parameters, I reclassified the original image into four edge type categories including clearcuts, other anthropogenic openings (agriculture and roads), brush, and natural openings (lakes, wetlands, grasslands).

Nest sampling.- Plots were gridded using flagging tape at 50 m intervals to enable mapping of territories and relocation of nest sites. Experienced nest searchers used traditional methods and thermal imaging (see Chapter 2) to locate nests on each study plot between 0530 and 1300 from 17 May through 28 July 2000. Nests were monitored every 2 to 4 days, checking for nest contents and recording parental behavior to determine nest fate. Once nests became inactive, I recorded their locations using a global positioning system (GPS). These locations were used to measure distances to nearest recent clearcut ≥ 5 ha, wetland and trail or road (Table 1).

Estimating nesting success.- Daily nest survival rates were determined by using the Mayfield estimate (Mayfield 1975) which accounts for the number of days nests were

observed. To minimize bias in this estimate, observation days for nests with uncertain fates were terminated on the last active date as described in Manolis et al. (2000). To calculate nest survival rates over the entire nesting period for Ovenbirds (*Seiurus aurocapillus*), a literature value of 25 days for the nest period length was used (Manolis 1999). We included observation days in survival estimates for all nests including those that had unknown fates or were abandoned. However, we only counted nest predation as a source of mortality. Thus, a given nest survival rate was equal to one minus the respective predation rate.

Ovenbird territory mapping.-While searching for nests, observers recorded locations of Ovenbirds on gridded plot maps and noted their behaviors, e.g. singing or calling. Observers visited each plot 12-23 times at intervals of two to four days in an effort to document fully each territory and cover the entire plot area evenly. Following International Bird Census Committee (1970) methods for territory mapping, movements of individuals, counter-singing events, and presence of females and fledglings were also noted. Information from all visits for each plot was combined onto a transparency, and delineations were drawn around clusters of observations and between countersinging males. A centroid of observations that fell outside a previously determined search area represented a territory that likely had the majority of its area outside of the plot, and these territories were not considered in the analyses (Fig. 2). This method enabled us to determine the density and breeding status of Ovenbird territories on each plot.

Ground cover measurements.-From 21 July through 3 August 2000, ground cover measurements were made around nests and around a non-use site that corresponded to specific Ovenbird nests. The non-use site was selected by pacing to the midpoint between two grid points so that the site was 1) within the corresponding mapped territory

to enable paired comparisons and 2) at least 15 m away from the active nest to avoid overlapping samples. If more than one midpoint was within the territory, the point was randomly selected.

Two 10 m length ropes were placed so that they were perpendicular and their centers intersected at each nest or non-use site to enable consistent percent cover measurements. Both ropes were marked at their centers and at 1 m and 5 m from their centers on each half. The 1 m scale was chosen to represent the nest substrate as this was the radius in which females would flush from the nest upon approach by observers. The 5 m scale was chosen to represent the surrounding microsite, as most nests were readily visible within this radius. Percent cover measurements were made separately within 1 m and 5 m of the center. The measurements included percent cover of sedges, dead woody stems, live woody stems, bare ground (including moss and exposed rock), leaves of live seedlings and forbs, and ferns < 50 cm high (Table 1). I estimated percent leaf litter cover by subtracting the sum of the other percent covers from 100. Measurements were made in an effort to quantify the visual qualities of the nest substrate and microsite. For example, percent sedge cover was measured by estimating the percent of ground visually obstructed by sedges. Rocks were often overgrown with moss, and both moss and rocks intermingled with exposed soil, so I categorized all these features as bare ground.

Determining source-sink status.-To determine the source-sink status of Ovenbird populations, three demographic parameters were used including annual mean number of fledged female offspring per adult in a population (fecundity), probability that the offspring survive to reproduce, and adult survival rate (Pulliam 1988). Annual Ovenbird fecundity was calculated in two different ways. For both methods, the mean number of females fledged per successful nest (assuming 50:50 sex ratio) for each plot was used.

The first method follows Donovan et al. (1995) and required nesting success estimates for each plot, number of potential broods, and number of potential nesting attempts. In calculating this measure of annual fecundity, the following assumptions were made: 1) maximum number of broods per female was one, 2) females renested once following nest failure on their first attempt, 3) fecundity was equal for all age classes, 4) nesting success was constant throughout season, and 5) mean fledged females per successful nest was constant throughout season (Donovan et al. 1995).

In addition to mean fledged females per successful nest, the second method required the number of adult females per plot and the proportion of fledged territories per plot. This method also requires assumptions 1, 3 and 5. The other assumptions are unnecessary because no nest success data were required. Furthermore, this method considers all failures by females to reproduce, while the first method is based on Mayfield calculations which considers only nest predation as a source for reproductive failure. We would expect the fecundity estimate based on territory fledging success to be equal to or lower than the one based on nest predation rates.

Statistical analyses.- Nests that were abandoned or that had ambiguous fates were omitted from the nest-level analyses. All nest site variables were tested for multivariate and univariate normality before conducting any tests. Nest variables included percent cover estimates, litter depths, and distances to edges (Table 2). Absolute values of differences in percent cover measurements and litter depth between 1 m and 5 m were also included. In addition, nest orientation, as well as distances to nearest trail, wetland and regenerating clearcut were included. Several of these variables failed to meet the assumptions of normality, and so stepwise logistic regression was used to select useful predictors of nest predation. Logistic regression does not assume that data are distributed

normally, and because of this the untransformed variables were tested in the regression model (Johnson 1998). All variables with an alpha less than 0.05 were entered into the stepwise logistic regression model.

Paired comparisons between percent cover measurements at Ovenbird nest sites and non-use sites were made using multiple analysis of variance (MANOVA), with a null hypothesis of no difference between sites and an alpha level of 0.05. Paired comparisons between percent cover measurements at the two spatial scales were also made using MANOVA. Both MANOVA tests were followed with paired *t*-tests for consistency (Johnson 1998) with an alpha level of 0.05 following a Bonferroni correction (Sokal and Rohlf 1995). I used the SAS procedures PROC LOGISTIC, PROC GLM, and PROC MEANS to conduct the logistic regression, MANOVA, and paired *t*-tests, respectively (SAS Institute 1990).

A chi-square statistic was used to compare daily survival rates using the computer program CONTRAST (Hines and Sauer 1989). Nests were ranked according to their distance to clearcut edge and assigned to distance categories in intervals of 18-20 nests per category.

Multiple linear regression was used to select landscape metrics that were useful predictors ($P < 0.1$) for the response variable. I inspected residual plots and normal plots to ensure that assumptions of statistical tests were met. The SAS procedure PROC REG was used to conduct the multiple linear regression (SAS Institute 1990).

RESULTS

Nest-level effects.-We located and monitored 88 active nests including those of the Ovenbird (n = 60), Hermit Thrush (n = 26; *Catharus guttatus*), Veery (n = 1; *Catharus fuscescens*), and Nashville Warbler (n = 1; *Vermivora ruficapilla*; Appendices 1 and 2).

Sample sizes were sufficient ($n \geq 27$ = number of predictors) for testing effects for all ground-nesting species ($n = 88$) and for Ovenbirds ($n = 60$). Of the nests that failed, predation was the primary cause of failure for all ground-nesting species ($n = 49$, 93.9%) and for Ovenbirds ($n = 31$, 90.3%). Four of the nests I monitored were abandoned, which may have resulted from disturbance by the Brown-headed Cowbird based on abandonment immediately following parasitism (*Molothrus ater*; one Ovenbird nest), inadvertent disturbance by human observers based on abandonment immediately following flushing the female from the nest (one Hermit Thrush nest), and female mortality based on the absence of a female in that territory following abandonment (two Ovenbird nests). Nest parasitism by Brown-headed Cowbirds on ground nests was low (5.7%), as only one Hermit Thrush nest and four Ovenbird nests were parasitized. Of the parasitized Ovenbird nests, only one fledged cowbird young.

The following model was selected for all ground nests at an alpha level of 0.05 using the stepwise procedure with logistic regression:

$$\text{logit}(p) = -1.04 + 0.11 \text{ FN5}$$

where p is the probability of nest predation and FN5 is percent fern cover within 5 m (Table 1). This model had the lowest Akaike's Information Criterion (AIC) of alternative models and percent concordance was moderate (66.5). This model indicated that predation risk increased with fern cover at the 5 m scale. For example, 3 of 52 fledged nests compared to 8 of 31 depredated nests had >15% fern cover (Fig. 2).

The following model was selected for Ovenbird nests at an alpha level of 0.05 using the stepwise procedure with logistic regression:

$$\text{logit}(p) = 0.40 + 0.18 | \text{DFN} | - 0.15 \text{ LD1} + 0.0006 \text{ DCC}$$

where DFN is the difference in percent fern cover between the 1 and 5 m scales, LD1 is

litter depth at 1 m, and DCC is distance to nearest clearcut (Table 1). This model had the lowest Akaike's Information Criterion (AIC) of alternative models and percent concordance was high (84.2).

The model indicated that nest predation risk increased with the difference in fern cover between the two scales. For example, one of 37 fledged Ovenbird nests compared to four of 18 depredated Ovenbird nests had >15% difference in fern cover (Fig. 3). The model also suggests that nests with deep litter had lower probability of predation. In support of this, nine of 18 depredated nests compared to eight of 37 fledged nests had litter depths under 15 mm (Fig. 4). The model also showed that nest predation risk increased with increasing distance from nearest clearcut. The frequency distribution of distances to clearcuts did not show a strong relationship, but five of 18 depredated nests compared to 15 of 37 fledged nests were within 400 m of clearcuts (Fig 5).

Nest site selection.-We recorded ground cover measurements for 45 non-use sites which were located within Ovenbird territories where an active nest was found (Appendix 3). There was no significant difference between percent cover measurements for used and non-used Ovenbird nest sites (MANOVA; $n = 45$, $df = 14$, $F = 1.58$, $P = 0.14$). A paired t -test for all variables showed that Ovenbird nest sites had lower percent live leaf cover ($P < 0.1$) and greater litter depth ($P = 0.01$) at the 1 m scale compared to non-use sites (Table 2). These results should be interpreted with caution because so many variables were tested.

Percent cover measurements for Ovenbird nests at the 5 m scale differed significantly from those at the 1 m scale (MANOVA; $n = 55$, $df = 7$, $F = 36.92$, $P < 0.0001$). As a consistency check, a paired t -test showed that percent cover of live wood, dead wood, moss and bare ground, and live leaf cover were greater at the 5 m scale (Table 3). Fern

cover was greater at the 5 m scale and percent litter cover was higher at the 1 m scale (Table 3). In general, percent total cover of the forest floor was less at the substrate scale.

Edge effects.- Distances to nearest trail and nearest wetland were not useful predictors of predation in the logistic regression model for ground nests. In contrast, distance to clearcut edge was a useful predictor of Ovenbird nest predation, but the relationship was unclear after inspecting the frequency distribution (Fig. 5). There was no detectable difference in nest survival rates between plots adjacent to clearcuts and plots far from clearcuts (ground-nesters: $X^2 = 0.04$, $df = 1$, $p = 0.84$; Ovenbirds: $X^2 = 0.29$, $df = 1$, $p = 0.60$).

To ensure that clearcut edges had no negative impact on nesting success, I compared daily nest survival rates across different distance to clearcut edge classes (Fig. 5). These classes were chosen to maximize the number of clearcut categories while maintaining a sufficient sample of nests in each category. Daily survival estimates did not differ among distance to edge classes for ground nesters ($X^2 = 0.32$, $df = 4$, $p = 0.99$) or for Ovenbirds ($X^2 = 2.32$, $df = 2$, $p = 0.31$).

Nest survival rates and fecundity.- Daily nest survival rates for all ground nesters ranged from 0.948 to 0.983 (Table 4) while Ovenbirds ranged from 0.952 to 0.994 on the six northern hardwood plots, and Hermit Thrushes had a nest survival rate of 0.959 (Table 5). In general, standard errors for daily survival rates were high within plots relative to differences among plots. Ovenbird fecundity as predicted from nest survival rates ranged from 0.90 to 1.82 fledged female per adult female, while fecundities as predicted from fledging success were between 1.43 and 1.81 (Table 5). These two measurements of fecundity were negatively correlated, but the relationship was not

significant ($r = -0.31$, $P = 0.54$).

Ovenbird territories.-We mapped and determined the breeding status of 219 Ovenbird territories on the six northern hardwood stands. Territory densities ranged from 0.98 to 1.79 males per ha (Table 6). Pairing success and fledging success of these territories ranged from 78.4 to 94.6% and 58.0 to 86.1%, respectively (Table 6). There was a highly positive relationship between pairing success and fledging success (Fig. 7; $r = 1.00$, $P < 0.0001$), and so these two variables will be treated synonymously hereafter. There was no relationship between Ovenbird nest survival rates and pairing success ($r = -0.26$, $P = 0.62$), territory density ($r = 0.03$, $P = 0.95$) or nest density ($r = 0.54$, $P = 0.27$). However, pairing success was negatively related to territory density (Fig. 7; $r = -0.83$, $P = 0.04$). Plots with high territory density tended to have low fledging success.

Landscape-level effects.- Percent mature forest across all seven buffers and all six plots averaged $53.1 \pm$ SD of 8.2 (range: 33.0, 80.3), mature forest edge density averaged 108.2 ± 11.1 m/ha (89.5, 129.5), and mean mature forest patch size averaged 9.1 ± 8.2 ha (3.8, 50.5). Percent mature forest was positively correlated with mean mature forest patch size at the 1 - 2.5 km buffers ($r > 0.79$, $P < 0.07$). Mature forest edge density was positively correlated with percent mature forest area at the 3 and 3.5 km buffers ($r > 0.91$, $P < 0.02$). None of the other buffer-specific landscape variables were related ($P > 0.1$).

Mature forest edge density within 1, 1.25 and 1.5 km of plot centers was a useful predictor for daily survival rates in multiple linear regression models for ground nests (Table 7). Survival rates decreased as edge density increased, indicating that plots with high predation rates had high amounts of edge in the landscape (Fig. 8). Mean mature forest patch size at the 3 km scale was a useful predictor (Table 7) and was positively related to daily nest survival rates for ground nesters (Fig. 8).

Mature forest edge density was also a useful predictor of Ovenbird fecundity, but only at the 1.25 and 1.5 km scales (Table 7). In both cases, edge density was negatively related to fecundity, and more importantly, high amounts of edge were associated with low fecundity (Fig. 9). Mature forest patch size was again a useful predictor, but at the 3.5 km scale (Table 7). Here, patch size was positively related to Ovenbird fecundity and plots with smaller patches had fecundities at or below the proposed source-sink threshold (Fig. 9). Despite mature forest edge density being a useful predictor for both ground nest survival rate and Ovenbird fecundity, none of the specific edge types were selected as useful predictors.

DISCUSSION

Similar substrate hypothesis.- The similar substrate hypothesis for Ovenbird nest predation was supported by my findings. Nests built on a unique substrate with respect to microsite fern cover may be more vulnerable to predators that forage among ferns. Although the result was not significant, average fern cover was greater at the 5 m scale. High fern cover characterized depredated ground nests of all species combined, but the similar substrate hypothesis was not supported for ground-nesters in general.

In South Carolina, Kilgo et al. (1996) studied Hooded Warblers (*Wilsonia citrina*), which nest approximately 1 m up in saplings, and found no support for the similar substrate hypothesis. However, they found that successful nests had more fern cover within 5 m than depredated nests. The authors proposed that Hooded Warblers conduct distraction displays and ferns may provide translucent cover that both enables predators to see the display but also protects the adult. Ovenbirds perform similar distraction displays (pers. ob.), but ferns may not serve the same function as they did for Hooded Warblers. These conflicting results could be explained by differences in predator

communities, or by the differences in vertical nest placement between the two species. Flaspohler et al. (2001a) noted that Ovenbirds may prefer to nest in areas with low levels of concealing vegetation.

Potential influences on elevated fern growth include foraging by white-tailed deer (*Odocoileus virginianus*; Rooney and Dress 1997, Fredericksen et al. 1998) and gaps in the forest canopy left by a fallen tree (Collins and Pickett 1988). This evidence suggests that areas with increased light levels may invoke conditions that attract mammals and induce fern growth. These events could conceivably lead to incidental predation on ground nests in microsites with high fern cover. There is a potential for bias in these inferences if the nests found in ferns were the ones most vulnerable to predation. For instance, nests built in fern thickets may have been hidden from observers and predators alike.

Litter depth effect.-Most Ovenbird nests built on substrates with shallow leaf litter in my study were depredated. Leaf litter depth may be positively correlated with insect biomass (Haskell 2000), and prey availability can influence the quality of Ovenbird territories (Burke and Nol 1998, Ortega and Capen 1999). Lower prey availability within a territory may cause the female to make more frequent foraging trips away from the nest, which could make the nest more vulnerable to predation (Zanette et al. 2000).

Alternatively, nest sites with deep litter (and higher insect abundance) may be limiting and thus occupied by the first Ovenbirds that return in the spring. Older individuals may have higher nesting success, possibly due to more experience at cryptic nest building (e.g., Martin and Roper 1988, Holmes et al. 1996). If this is true, then this would violate the assumption in calculations of fecundity that survivorship is equal among age classes. It should be noted that litter depth may not be an important influence on nest predation in

all northern hardwood stands (see Manolis 1999).

Nest site selection.-According to my comparisons of used and non-used sites, Ovenbirds did not select areas within their territories with lower fern cover, but nest sites did have deeper leaf litter on average, although the latter result may be spurious. It is possible that Ovenbirds nest in territories that are homogenous with respect to these characteristics. Ovenbird nest sites had less live leaf cover than non-use sites. Leaf cover could create shady and thermally inadequate nest sites, or leaves may be visual barriers to performing successful predator-distraction displays. Alternatively, observers may have missed nests built in heavy leaf cover. Ovenbirds nested on substrates that had low amounts of herbaceous cover, live and dead woody cover and moss and bare ground relative to the surrounding microsite. These sites may have been selected to minimize visual obstructions near the nest to improve vigilance for oncoming predators.

Edge effects.- According to a logistic regression model, Ovenbird nests built far from clearcut edges were more likely to be depredated on my study plots. However, comparisons of nest survival rates among distance to edge categories showed that there was no edge effect. The former result appears anomalous and could have occurred by chance because nests were sampled unevenly along the distance gradient. Flaspohler et al. (2001b) and Manolis (1999) studied Ovenbird nesting success as a function of distance to clearcut edge in northern hardwoods of northern Minnesota and Wisconsin, respectively. They both found that distance to clearcut edge was a useful predictor of Ovenbird nest predation, and that nests near clearcut edges had a higher probability of predation. Their nest samples were distributed evenly across distance classes, with a high sample size within 300 m of clearcuts.

Depredated ground nests of all species combined were not characterized by clearcut

proximity, and ground nest survival rates were consistent across distance to clearcut edge classes. In contrast, depredated Ovenbird nests were characterized as being far from clearcut edges on my study plots. Other studies investigating effects of clearcut proximity on Ovenbird nesting success had contrasting results. King et al. (1996) found that Ovenbird nest predation rates were higher within 200 m of clearcut edges in New Hampshire, and both Flaspohler et al. (2001b) and Manolis (1999) found that Ovenbird nest predation rates were higher within 300 m of clearcut edges in Wisconsin and Minnesota, respectively. The eastern chipmunk (*Tamias striatus*) is a potential nest predator in northern hardwoods (e.g., Fenske-Crawford and Niemi 1997), and this species spends less time foraging in areas adjacent to clearcuts than in continuous forests (Mahan and Yahner 1999). However, small mammals have been reported to be more abundant in mature forest within 350 m or less of clearcut edges, including eastern chipmunks and red squirrels (*Tamiasciurus hudsonicus*) (King et al. 1998), red-backed voles (*Clethrionomys gapperi*), and deer mice (*Peromyscus maniculatus*) (Sekgororane and Dilworth 1995).

There are at least two explanations for higher nest predation near clearcut edges. Mammalian predators may avoid dense clearcuts (King et al. 1998). They may instead pass through the relatively unobstructed understory of adjacent forests, depredating nests incidentally along the way (e.g., Vickery et al. 1992). Another possibility is that prey density may be greater near clearcut edges, including songbird nests (Flaspohler et al. 2001b) and small mammals (Sekgororane and Dilworth 1995, King et al. 1998). This elevated prey density could attract nest predators in general to areas near clearcuts.

The conflicting results between my study and other similar studies indicates that distance to a single clearcut edge may be insufficient to assess silvicultural effects on ground nest predation. Rather, considering edge density within the landscape may be

more important for addressing edge effects. Perhaps nest predators are abundant in areas beyond 350 m from clearcuts on my study plots and respond to habitat characteristics other than clearcut edge (e.g., proximity to agricultural edge). In addition, studies testing the edge-effect hypothesis using artificial ground nests have had inconsistent results (Hartley and Hunter 1998). More knowledge about nest predator foraging preferences is needed before making any general conclusions about edge effects on nesting success of ground-nesting forest songbirds.

Nest survival rates and fecundity.-The range of survival rates for ground nesters on my study plots (0.948, 0.983) was similar to that found in northern hardwoods of the Chippewa National Forest (NF) in northern Minnesota (0.951, 0.974) (Manolis unpubl. data) and less extreme than the range found in northern hardwood forests of the Nicolet NF in northeastern Wisconsin (0.938, 0.995) (Flaspohler 1998). The overall Hermit Thrush nest survival rate was intermediate for my study (0.959), lowest in the Chippewa NF (0.946) (Manolis unpubl. data), and greatest in the Nicolet NF (0.962) (Flaspohler 1998). The range of Ovenbird nest survival rates on my plots (0.952, 0.994) overlapped with both those found in Chippewa NF (0.95, 0.979) (Manolis unpubl. data) and in Nicolet NF (0.938, 1.0) (Flaspohler 1998).

Following Donovan et al. (1995), an adult survival estimate of 0.623 and juvenile survival of 0.31 for Ovenbirds would require ≥ 1.2 fledged females per adult female per year to maintain a stable or growing population. Ovenbird fecundity based on nest survival estimates across all of my plots (1.65) indicates that the population as a whole is likely a source (fecundity > 1.2), but the variability in my estimates creates some uncertainty in this conclusion. My Ovenbird fecundity estimate was similar to that of edge habitat in Nicolet NF (1.69) and greater than that for overall fecundity in Chippewa

NF (1.16). My highest fecundity value based on the nest survival estimate (1.81) was below that for interior habitat in Nicolet NF (1.93).

If both methods for estimating fecundity were accurate, I would expect to see the estimate based on nest survival rates, with only predation as a source of mortality, to be equal to or greater than the estimate based on actual fledging success of territories with females. The method based on fledging success represented the proportion of territories that fledged relative to those that failed due to all sources, not just predation. Thus, estimates of fecundity are expected to be higher using the fledged territory method. However, my fecundity estimates using the fledged territory method were less than those using the nest survival method for two plots, greater on three plots and similar on only one of the six plots. In addition, the two estimates were uncorrelated.

One possibility for this inconsistency is that Ovenbirds reneest more than once on average on some study plots, and only once or none at all on others. I did observe up to three nests in an Ovenbird territory, albeit some of which were inactive upon discovery. Another possibility is that Ovenbirds may occasionally produce two broods (Van Horn and Donovan 1994). In support of this, I observed two Ovenbird nests that fledged young consecutively within a single territory. It should be noted that both overall fecundity estimates for Ovenbirds were similar (approximately 1.6), which indicates that these methods may be equally reliable for a range of study sites.

Ovenbird territories.- Ovenbird densities on my sites were high. These sites were similar to or twice the density of those found in large (> 2000 ha) maple woodlots of southern Ontario (Burke and Nol 1998) and in contiguous tracts of maple in Green Mountain NF, Vermont (Buford and Capen 1999). Pairing success in this study was high and similar to those found in woodlots with large core areas (>40 ha, 100 m from edges)

in southern Ontario (Burke and Nol 1998), in contiguous forests of both central Pennsylvania (Rodewald and Yahner 2000) and Green Mountain NF, Vermont (Ortega and Capen 1999). Our lowest fledging success estimate was greater than the average fledging success of Ovenbirds in Green Mountain NF (Ortega and Capen 1999) and similar to that in unfragmented forests of southern Missouri (Porneluzi and Faaborg 1999).

Ovenbird territory densities were not related to nest survival rates in this study, which is consistent with results from central Pennsylvania (Rodewald and Yahner 2000), but these were positively related in southern Ontario. Pairing success was negatively correlated with territory density on my sites, while these were positively correlated in southern Ontario (Burke and Nol 1998). My range of densities was greater than that in Ontario, and therefore there may be a density threshold upon which pairing success begins to decline. Hagan et al. (1996) found that Ovenbird male densities were greater and pairing success was lower in landscapes with high amounts of recent clearcuts compared with those in contiguous mature forest. Male Ovenbirds that previously maintained territories in now clearcut areas must move into areas that were not clearcut, resulting in elevated Ovenbird densities and consequent low pairing success in the neighboring mature forest (Hagan et al. 1996). The mechanism for low pairing success in areas with high male densities is unclear. In any case, the strong relationship that I found between pairing and fledging success indicates that Ovenbird females may be limiting the fitness of individual males.

I found no relationship between nest density and daily nest survival rates of Ovenbirds. In contrast, Flaspohler et al. (2001b) found that Ovenbird nest densities were higher and nest survival rates were lower near clearcut edges, suggesting an ideal free

distribution along a distance gradient. Perhaps this phenomenon occurs only near habitat edges. It should be noted that the validity of conclusions from these patterns depends on the assumption that nest samples were representative of the actual density of nests.

Landscape-level effects.- For both all ground nesters and Ovenbirds alone, nest survival rates were lowest in areas of high mature forest edge density within 1.25 and 1.5 km. Knutsen et al. (unpubl. data) studied low-nesting songbirds in oak-hickory stands of southeastern Minnesota and found no relationship between nest survival rate and forest edge density within 1, 5 or 10 km. Perhaps edge density within 1 - 1.5 km is critical for detecting this relationship.

The appropriate scales of measurement for ecological processes are generally unknown (e.g., Morris 1987). For my study, percent forest cover was generally correlated with mean forest patch size and nest survival rates increased with mean patch size at larger buffer widths. This result is consistent with investigations at large (5-10 km) scales in southeastern Minnesota (Knutsen et al. unpubl. data), southern Ontario (Burke and Nol 2000), and midwestern U.S. (Robinson et al. 1995). According to these findings and my own, maintaining large patches of forest is important at larger scales, but minimizing edge at smaller scales is also important for nest survival.

With a sample of six plots and high variances for the estimates of daily survival rates, statistical power was probably low. Thus, landscape variables that affected reproductive success of ground nesters may have been undetected. These landscape-level analyses were exploratory and should be interpreted with caution. Further investigation using more replicates and a wider range of landscape conditions is necessary to further test the initial hypotheses.

Tewksbury et al. (1998) studied shrub and tree-nesters in conifer stands within

forested and agricultural landscapes of western Montana and found that nest predation rates were higher in predominantly forested landscapes than in agricultural landscapes. They also found that red squirrels were more abundant in forested landscapes, and they proposed that these and other forest-dwelling nest predators were driving the relationship. Andrén (1992) studied predation on artificial ground nests in coniferous forests of south-central Sweden and found that both corvid density and nest predation increased with proportion of agricultural land cover. This is consistent with results in the midwestern U.S. (e.g., Robinson et al. 1995). The proposed mechanism for this relationship was that habitat generalist corvids were important nest predators along woodlot edges. Predator assemblages appear to be an important factor in determining the relationship between forest cover and nest predation.

Studies investigating landscape effects on nest predation in silvicultural landscapes are rarer but have found similar relationships. Yahner and Scott (1988) studied ground and arboreal artificial nests in managed aspen stands of Pennsylvania and found that both nest predation and corvid density were highest in areas with the greatest amount of aspen clearcuts. Results from studies using artificial nests should be interpreted with caution, but artificial nests may provide indices of nest predation in different landscapes (Wilson and Brittingham 1998).

The qualities of the non-forested portion of the landscape matrix may relate to predation levels on forest songbird nests. The landscape of northern Minnesota is characterized as having mixed coniferous and hardwood species that are part of a naturally heterogeneous matrix consisting of lakes, rivers, forested wetlands and nonforested wetlands (Mladenoff et al. 1997). The landscape is also perforated by human-modified components including regenerating clearcuts, roads, pastures, lawns and

houses (Mladenoff et al. 1997, Minnesota Department of Natural Resources 1999). Of the edge types that I considered, no single edge type in the matrix induced elevated nest predation levels. Landscapes with high edge densities may simply have high predator levels due to high levels of habitat heterogeneity. More studies investigating relationships between landscape composition and configuration on natural nest predation in naturally heterogeneous, silvicultural landscapes are needed to increase understanding of the impacts of management practices on forest songbird populations.

Regional effects.-The results of my study should be considered within the context of the region studied. Forests along the southern boreal-northern hardwood border of North America historically experienced disturbance regimes that depended on the species composition of individual stands. Conifer-dominated stands experienced frequent fires that varied in size while stands composed of mostly northern hardwoods experienced infrequent fires and windthrows (Pastor and Mladenoff 1992). These historical disturbances and subsequent forest succession produced diverse stands in the boreal-northern hardwood transition zone (Pastor and Mladenoff 1992). Migratory birds breeding in these forests may be adapted to disturbances and thus may be resilient following clearcutting (Hunter 1992, Niemi et al. 1998), which may resemble burning or windthrows to some degree (Schmiegelow et al. 1997). However, temporally and spatially frequent anthropogenic disturbances may have created more homogeneous forest cover types across landscapes (Mladenoff and Pastor 1993). Consequently, songbird breeding productivity in these patches may be sensitive to current anthropogenic disturbance regimes.

Multi-scale effects.-Habitat features at different spatial scales affect nesting success, and this may influence breeding productivity of forest songbirds. The landscape context

for breeding songbirds can have an influence on metapopulation dynamics at a regional scale. Songbird populations breeding in large contiguous tracts of boreal regions and of southeastern Missouri may serve as sources for population sinks breeding in forest fragments within agricultural landscapes of east-central North America (Robinson et al. 1995, Flaspohler 1998). However, sinks may exist in areas adjacent to clearcuts in the boreal-hardwood forests (Manolis 1999). The proposed mechanisms for the source-sink phenomenon in songbird populations include elevated parasitism and predation rates in landscapes fragmented by agriculture (Brittingham and Temple 1983, Robinson et al. 1995, Donovan et al. 1995) and elevated predation rates in landscapes fragmented by silviculture (Manolis 1999).

Complex interactions between spatial and temporal scales could explain the opposing results from landscape-level studies in Montana (Tewksbury et al. 1998) and the midwestern United States (e.g., Robinson et al. 1995). Adaptations of songbirds to heterogeneity formed by frequent fires in coniferous forest may explain contrasting results in why predation was lower in forested areas. The historically patchy landscape of the Montana study area due to fires and flooding could contribute to their results (Tewksbury et al. 1998). Another probable influence was the greater density and different assemblage of nest predators in the forest-dominated landscape. More research is needed that investigates effects of fragmentation on nesting success in different regions to test the generality of the relationship.

The properties of the surrounding matrix modify the edge effect on nest predation within a patch. For example, edge effects observed in agricultural landscapes differ from those in forested landscapes (Andrén 1995). In addition, the age of regenerating clearcuts may influence edge effects within adjacent patches (Fenske-Crawford and

Niemi 1997). These differences may relate to the distribution and abundance of alternate prey for nest predators.

Likewise, patch characteristics can influence microsite quality within that patch. Litter depth within Ovenbird territories may increase with increasing woodlot size (Burke and Nol 1998). Tree fall gaps caused by selective logging in a patch may induce elevated light levels, modify microsite qualities such as fern growth (Collins and Pickett 1988), and ultimately induce elevated nest predator activity in those microsites.

Conservation implications.- High probability of nest predation may be related to microsite qualities such as high amounts of fern cover, which may be induced by heavy deer browsing (Rooney and Dress 1997, Fredericksen et al. 1998), and shallow leaf litter, which may be induced by low humidity found in small forest patches (Burke and Nol 1998) or by earthworm infestations (Burtelow et al. 1998). While proximity to the nearest edge alone may not always influence probability of nest predation, my results indicated that edge density exceeding 110 m/ha within a 1.25 - 1.5 km radius may create sink habitat for Ovenbirds. Likewise, mean forest patch size below 6 ha within a ≥ 3 km radius may create sink habitat for Ovenbirds.

Properties of microsites, patches, landscape composition and the regional context can influence breeding productivity of ground-nesting forest songbirds. However, there may be a danger in maintaining habitat features at a limited scale. Songbird productivity could still be low in a landscape with a high proportion of forest cover at large scales and low edge density at finer scales if microhabitats within forest stands provide nesting sites that are vulnerable to predation.

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TABLE 1. Variable names for habitat measurements used in statistical analyses. Percent ground cover and litter depth measurements were made at 1 and 5 m from each nest (e.g., PS1 and PS5). The difference between measurements for use and non-use sites were used to test for site selection within territories (e.g., DPS1 and DPS5). The difference between measurements at two scales was used to describe scale-dependent nest site selection (e.g., PS1 - PS5 = DPS), and the absolute value of the difference was used to test the similar substrate hypothesis (e.g., $|DPS|$).

Measurement	Variable name
Percent ground cover	
Litter	LT1, LT5, DLT1, DLT5, DLT
Sedges	S1, S5, DS1, DS5, DS
Dead woody stems	DW1, DW5, DDW1, DDW5, DDW
Live woody stems	LW1, LW5, DLW1, DLW5, DLW
Moss and bare ground	MB1, MB5, DMB1, DMB5, DMB
Seedling leaves and forbs	LF1, LF5, DLF1, DLF5, DLF
Ferns	FN1, FN5, DFN1, DFN5, DFN
Litter depth (mm)	LD1, LD5, DLD1, DLD5, DLD
Nest orientation (degrees)	ORNT
Distances to edges (m)	
Trail	DTR
Wetland	DWET
Regenerating clearcut	DCC
Percent forest cover	PFOREST
Forest edge density (m/ha)	FOREEDGE
Average forest patch size (ha)	FORPATCH

TABLE 2. Results from paired *t*-tests comparing used and non-used Ovenbird nest sites in Aitkin County, Minnesota ($n = 45$). Negative means indicate that values for non-used sites were on average greater than those for used sites. The null hypothesis for all tests was $\mu = 0$. Variables highlighted in bold were statistically meaningful ($P < 0.1$, $P'' < 0.006$) following a Bonferroni correction.

Measurement	Mean \pm SE	<i>P</i>
DLT1	-0.44 \pm 2.20	0.843
DLT5	3.95 \pm 1.93	0.046
DS1	3.59 \pm 1.96	0.074
DS5	-2.16 \pm 1.93	0.269
DLW1	-0.41 \pm 0.31	0.187
DLW5	-0.23 \pm 0.25	0.353
DDW1	-0.84 \pm 0.89	0.354
DDW5	-1.03 \pm 0.83	0.220
DMB1	-2.28 \pm 1.35	0.098
DMB5	-0.52 \pm 0.79	0.513
DLF1	-7.40 \pm 2.49	0.005
DLF5	-5.02 \pm 2.54	0.054
DFN1	-0.15 \pm 1.41	0.914
DFN5	-2.31 \pm 1.71	0.183
DLD1	5.82 \pm 2.17	0.010
DLD5	-0.33 \pm 2.18	0.881

TABLE 3. Results from paired *t*-tests comparing Ovenbird percent cover measurements at 1 m and 5 m scales in Aitkin County, Minnesota ($n = 55$). The null hypothesis for all tests was $\mu = 0$. Variables highlighted in bold were statistically meaningful ($P < 0.1$, $P'' < 0.0125$) following a Bonferroni correction.

Measurement	Mean \pm SE	<i>P</i>
DPLT	5.98 \pm 1.27	<.0001
DPG	1.43 \pm 1.06	0.18
DPLW	-3.21 \pm 0.22	<.0001
DPDW	-2.08 \pm 0.59	0.0008
DPMB	-2.12 \pm 0.49	<.0001
DPLF	-8.99 \pm 1.47	<.0001
DPFN	-1.92 \pm 0.78	0.02
DLTD	0.38 \pm 0.87	0.67

TABLE 4. Mayfield calculations for ground nests in northern hardwoods of Aitkin County, Minnesota.

Plot/Group	Obs. ^a	Nests	No. Depred. ^c	DSR ^d	SE ^e
Beaver	348.5	24	8	0.98	0.01
Jewett	178.0	15	5	0.97	0.01
Kim	97.0	9	5	0.95	0.02
Mill	181.5	12	3	0.98	0.01
Pliny	116.5	12	5	0.96	0.02
Rice	214.0	15	5	0.98	0.01

^a Total number of days all nests were observed.

^b Number of nests depredated.

^c DSR = 1 - Depred/Obs Days

^d Standard error of DSR

TABLE 5. Daily survival rates (DSR) and nest survival rates (NSR) for Ovenbird and Hermit thrush nests and fecundity estimates for female Ovenbirds in northern hardwoods of Aitkin County, Minnesota.

Plot	Obs. Days ^a	Nests	Depred. ^b	DSR ^c	SE ^d	NSR ^e	Fecundity ^f	
							Model ^g	Observed ^h
Ovenbird								
Beaver	240.5	16	6	0.975	0.010	0.532	1.56	1.50
Jewett	142.5	10	2	0.986	0.010	0.702	1.82	1.43
Kim	76.5	7	4	0.948	0.025	0.261	0.91	1.63
Millward	162.5	10	1	0.994	0.006	0.857	2.01	1.79
Pliny	63.0	7	3	0.952	0.027	0.295	1.26	1.81
Rice Lake	136.0	10	3	0.978	0.013	0.573	1.50	1.62
All plots	821.0	60	19	0.977	0.005	0.557	1.65	1.63
Hermit Thrush								
All plots	290.5	26	12	0.959	0.012	0.294	-	-

^a Total number of days all nests were observed.

^b Number of nests depredated.

^c $DSR = 1 - \text{Depred}/\text{Obs Days}$

^d Standard error of DSR

^e Ovenbird: $NSR = DSR^{25}$; Hermit Thrush: $NSR = DSR^{29}$

^f Number of female fledglings per adult female; 1.2 needed to maintain stable population

^g Values calculated from NSR, based on 2 nesting attempts and a population of 100 females

^h Values calculated from observed fledging success of territory owners

TABLE 6. Density (No. males per ha), pairing success, and fledging success of Ovenbird territories in northern hardwoods of Aitkin County, Minnesota.

Values in parentheses are number of territories.

Plot	No. Visits	Area (ha)	Density	Paired (%)	Fledged (%)
Beaver	12	28	1.79 (51)	78.4 (51)	58.0 (50)
Jewett	18	26	1.39 (36)	88.9 (36)	74.3 (35)
Kim	12	20	1.69 (34)	82.4 (34)	58.8 (34)
Mill	17	23	1.23 (28)	85.7 (28)	64.3 (28)
Pliny	16	38	0.98 (37)	94.6 (37)	86.1 (36)
Rice	23	25	1.32 (33)	93.9 (33)	81.8 (33)

TABLE 7. Multiple linear regression models of landscape metrics used to predict daily survival rates of ground nests and Ovenbird fecundity in northern hardwoods of Aitkin County, Minnesota. All variables entered were significant with an alpha level of 0.1.

Buffer Radius			
(km)	Model	R^2	P
Ground nest daily survival rate			
1.00	1.06-0.0009 FOREEDGE	0.61	0.07
1.25	1.11-0.001 FOREEDGE-0.03 FORAREA ^a	1.00	< 0.01
1.50	1.08-0.001 FOREEDGE	0.86	< 0.01
2.00	-	-	-
2.50	-	-	-
3.00	0.92+0.83 FORPATCH	0.60	0.07
3.50	-	0.83	-
Ovenbird fecundity			
1.00	-	-	-
1.25	4.98-0.03 FOREEDGE	0.87	0.01
1.50	4.69-0.03 FOREEDGE	0.80	0.02
2.00	-	-	-
2.50	-	-	-
3.00	-	-	-
3.50	0.10+0.00002 FORPATCH	0.56	0.09

^a Partial R^2 values for FOREEDGE and FORAREA in this model were 0.9445 ($p=0.0012$) and 0.0546 ($p=0.0008$), respectively.

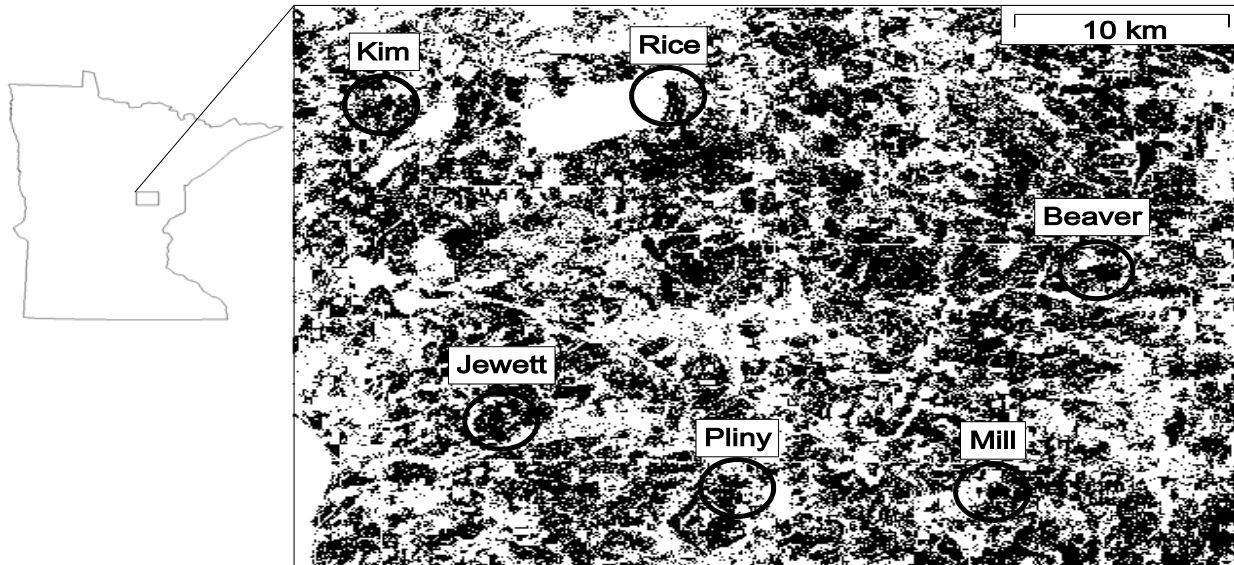


FIG. 1. A 30 m resolution image derived from LANDSAT data showing six northern hardwood stands located in southern Aitkin County, Minnesota. Black areas represent mature forest, and white areas represent cover types other than mature forest. Plots are indicated by black circles and plot names are given.

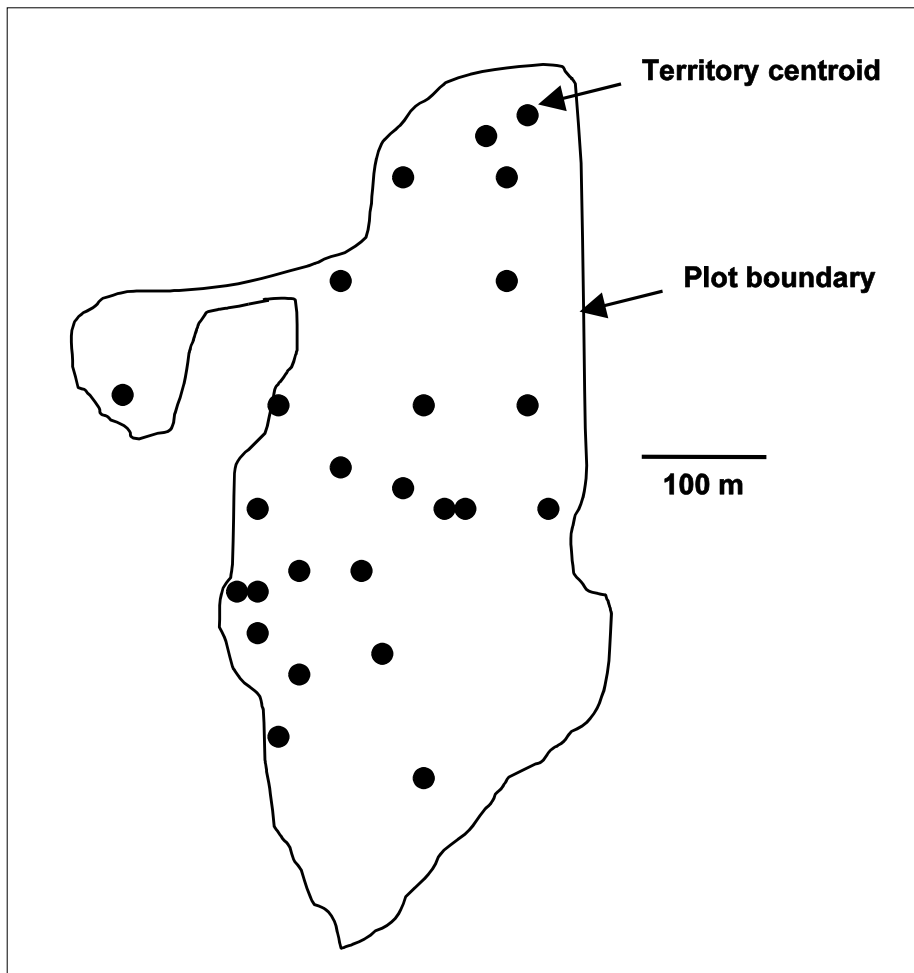


FIG. 2. Ovenbird territory map for Mill plot within a northern hardwood stand in Aitkin County, Minnesota. Each black dot represents the centroid of observations for a territory.

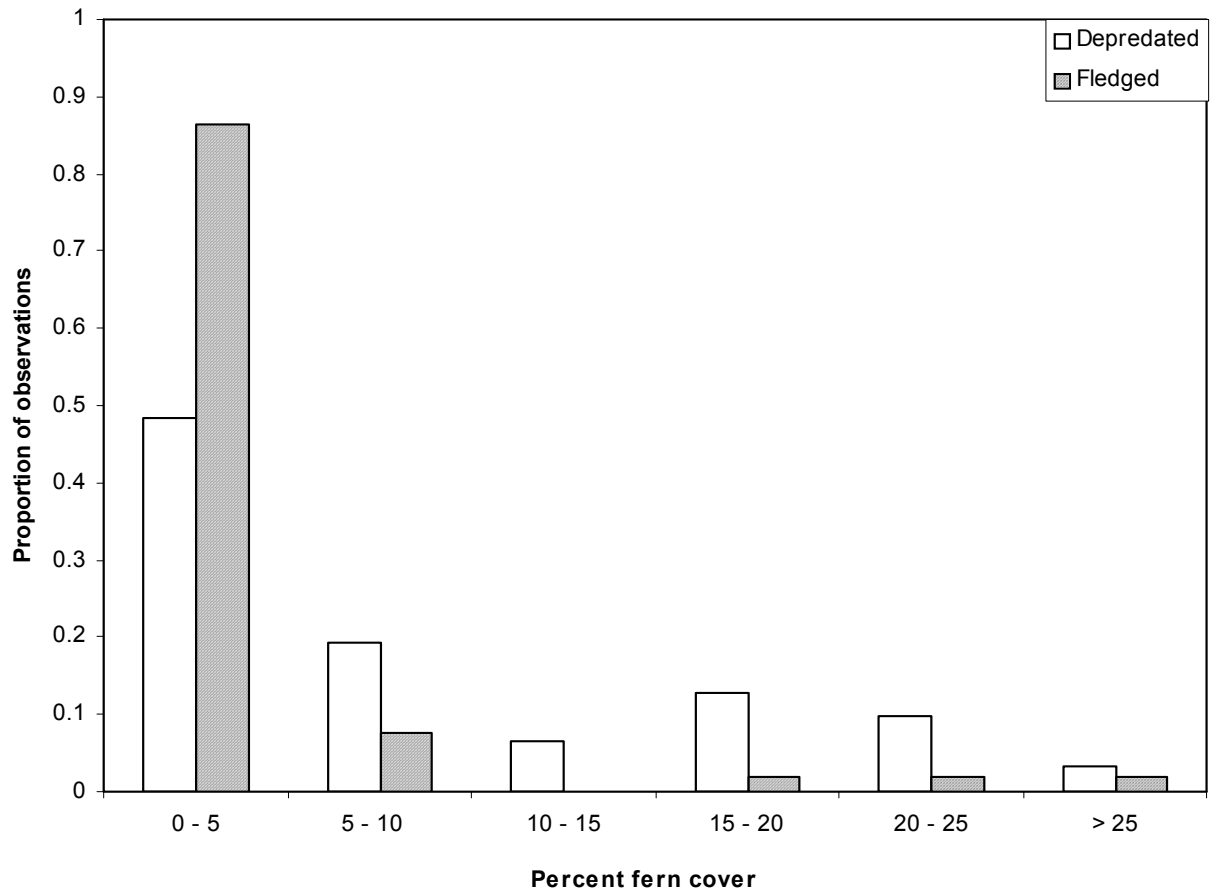


FIG. 3. Comparison between distributions of percent fern cover observations for depredated ($n = 31$) and fledged ($n = 52$) ground nests. Fern cover observations were made within 5 m of nests.

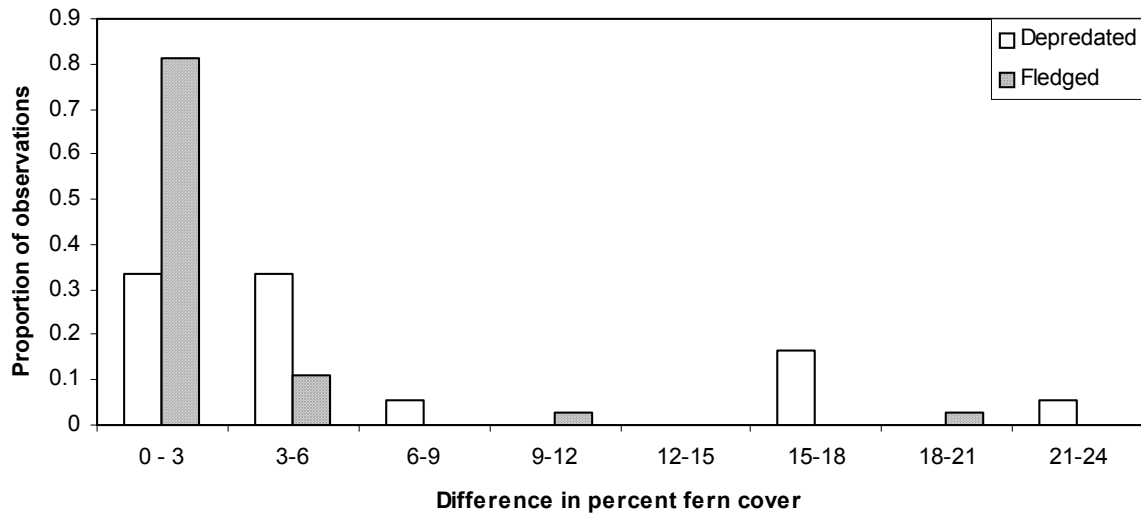


FIG. 4. Comparisons of the frequency distributions for absolute values of differences in percent fern cover for depredated ($n = 18$) and fledged ($n = 37$) Ovenbird nests. For each nest, the value for percent fern cover within 5 m was subtracted from the value within 1 m of the nest.

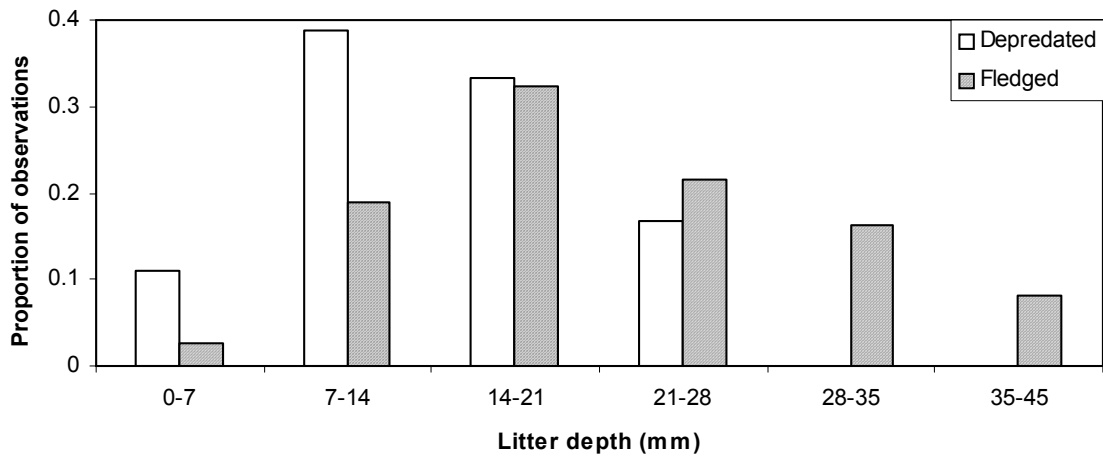


FIG. 5. Comparisons of the distributions of litter depth for depredated ($n = 18$) and fledged ($n = 37$) Ovenbird nests. The heights above the axis represent the proportion of litter depth observations at the 1 m scale.

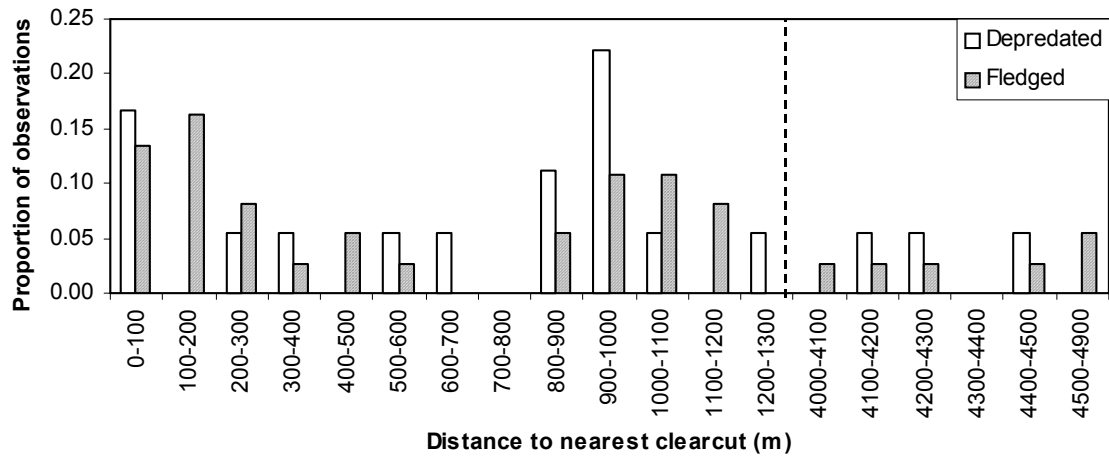


FIG. 6. Comparisons of the distributions of distances to nearest clearcut for depredated ($n = 18$) and fledged ($n = 37$) Ovenbird nests. Dashed line indicates gap in range of distance categories.

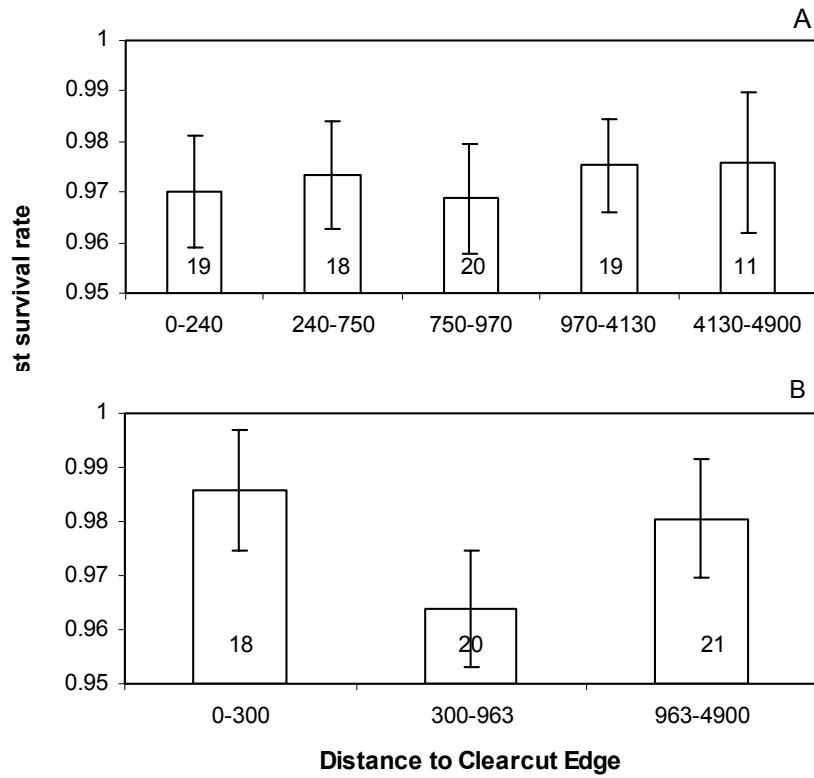


FIG. 7. Regenerating clearcut edge effects on daily survival rates of all ground nests (A) and Ovenbird nests (B) in northern hardwoods of Aitkin County, Minnesota. Error bars are standard errors, and values at the bases of the bars are numbers of nests.

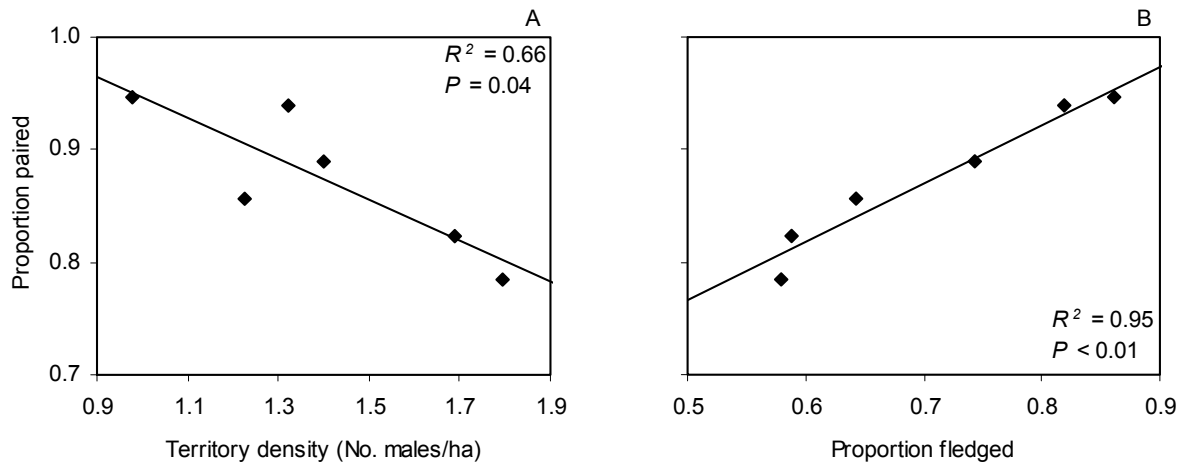


FIG. 8. Relationships between Ovenbird pairing success and both territory density (A) and fledging success (B) in northern hardwoods of Aitkin County, Minnesota. Each point represents one study plot. Line of best fit determined by linear regression. Lines of best fit determined by linear regression (A: $y = -0.3236x + 1.1589$; B: $y = 1.8179x - 0.8819$).

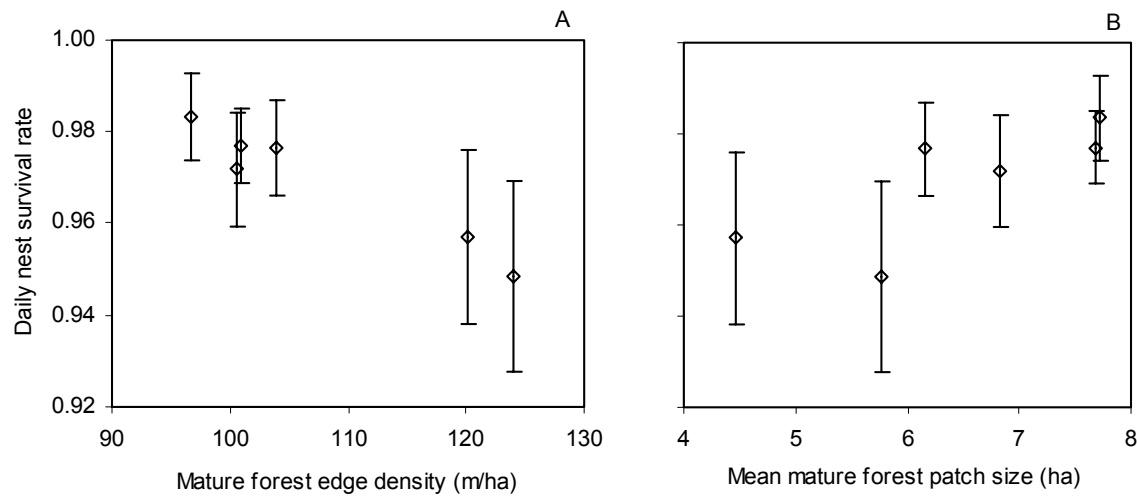


FIG. 9. Relationships between daily survival rates of ground nests and both mature forest edge density at 1.25 km buffer (A) and mean patch size at the 3 km buffer (B) in northern hardwoods of Aitkin County, Minnesota. Each point represents one study plot and whiskers denote one standard error. For example, triangles represent edge density within 1.00 km of each plot center.

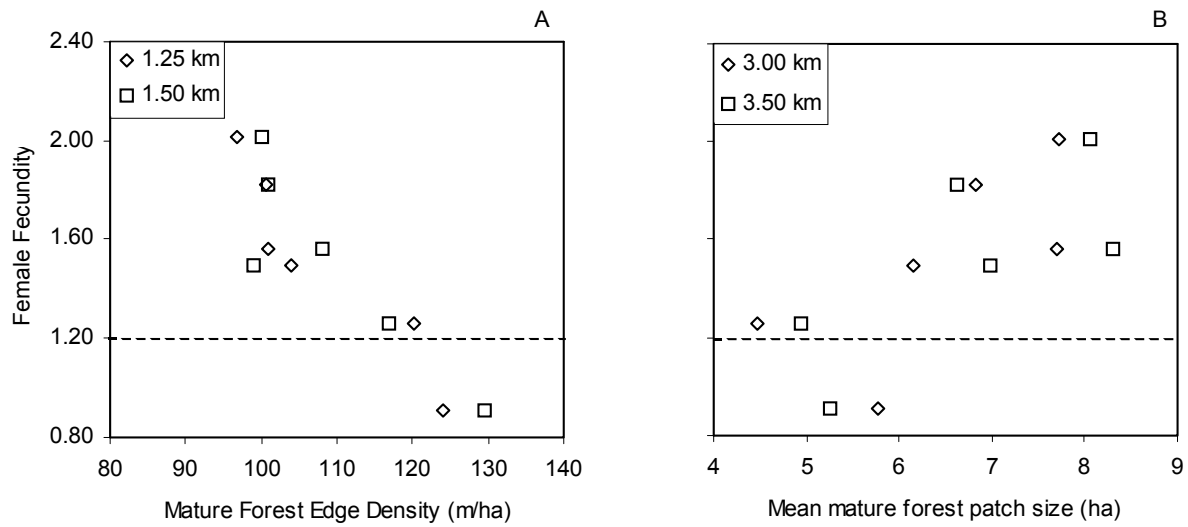


FIG. 10. Relationships between Ovenbird fecundity and both mature forest edge density (A) and mean patch size (B) in northern hardwoods of Aitkin County, Minnesota. Each point represents one study plot for different spatial scales. For example, diamonds represent edge density within 1.25 km of each plot center. The dashed line represents the source-sink threshold of 1.2, following Donovan et al. (1995).

**CHAPTER 2: USEFULNESS OF FAR INFRARED THERMAL IMAGING FOR
STUDYING BREEDING BIOLOGY OF SUBCANOPY-NESTING FOREST
SONGBIRDS**

Abstract.--In an effort to improve nest finding techniques, the application of far infrared (FIR) thermal imaging to locate nests was investigated. A thermal imaging camera NIGHTSIGHT PalmIR 250 was tested as a tool to find nests of ground-nesting songbirds in northern hardwood forests. The thermal imager helped locate 2 of 21 Ovenbird nests and 0 of 15 thrush nests. Usefulness of the camera was limited by cryptic adult behavior and by the awkward camera interface. Despite the limited ability to locate nests, the device was useful for locating fledged young. Thermal imaging has potential for further development in locating nests of forest birds that exhibit vigorous nest defense behavior or of those that nest on steep slopes.

INTRODUCTION

Locating and monitoring many songbird nests is essential to understand their life history characteristics, demographics and population trends. Traditional methods of finding nests involve searching for nests by using a search image and following females to their nests (Martin and Geupel 1993). These tactics may be similar to those used by nest predators (see Flaspohler 1998) and thus could lead to some bias. Human observers typically cannot locate all nests in an area and may only locate the more obvious nests. In particular, nests located by observers also may be those more vulnerable to visually-oriented predators (Vickery et al. 1992). Nest finding methods that are independent of those used by such nest predators are necessary to reduce bias and to improve estimates of nest predation rates. In addition, studies investigating breeding biology have had insufficient sample sizes, and hence low statistical power, to adequately test hypotheses (see Manolis 1999).

Far infrared (FIR) thermal imaging devices may hold potential for both reducing bias in nesting studies and increasing sample sizes. These devices are portable and possess sensors that convert thermal radiation into visible images (Raytheon 1999). This technology was useful for locating Lapland Longspur (*Calcarius lapponicus*) nests in arctic tundra when their approximate location was known (Boonstra et al. 1995). To my knowledge, there have been no other studies that have investigated the usefulness of FIR thermal imaging for locating songbird nests. I assessed the effectiveness of FIR thermal imaging for detecting thermal radiation emitted by nests heated by songbirds nesting in the forest subcanopy.

METHODS

I field tested the NIGHTSIGHT PalmIR 250 (manufactured by Raytheon Systems Company in Dallas, Texas; distributed by Pro Action in Minnesota: 1-800-290-1137), a thermal imaging camera that was designed for field uses (Raytheon 1999). To test the potential effectiveness of the device, I heated objects using my hands and hid them in leaf litter. These objects emanated sufficient heat to allow detection with the device from up to 15 m away. In addition, I viewed several passerine species with the device, and they radiated heat that enabled us to follow them readily through forested areas. I was confident that the device had some potential for locating nests of forest songbirds.

The FIR device was used daily between 1 June and 7 July 2000, and most often on cloudy days or between 0530 and 0800 on clear days. I tested the device as a tool to help find nests and fledglings of the Ovenbird (*Seiurus aurocapillus*), Hermit Thrush (*Catharus guttatus*), and Veery (*Catharus fuscescens*) in two northern hardwood stands of east-central Minnesota. While searching for nests or fledglings, the device was employed when an adult appeared or when a nest or fledgling was suspected to be near.

RESULTS AND DISCUSSION

While searching for nests and carrying the thermal imager, I located 19 Ovenbird nests, of which two were first spotted with the thermal imager. I located 15 other ground nests and 5 above-ground subcanopy nests, all of which were located without the aid of the device (Table 1).

The first of two Ovenbird nests was in early nestling stage and was located while scanning for a Hermit Thrush nest after an adult Hermit Thrush perched near the observer. The nest was 10 m away and its opening was oriented toward the observer

when it was spotted with the device. The dome of some Ovenbird nests radiated heat from the incubating adult even while the adult was off the nest. This phenomenon probably facilitated locating this nest. The second Ovenbird nest was positioned on a steep slope (approximately 30E) and the opening was oriented downhill. In addition, both adults scolded persistently while the observer was near the nest. The nest was readily visible from most downhill locations and was visible up to 30 m away.

There are three possible reasons for the low success of using the thermal imager to locate nests. One possible explanation was the lack of adult behavior around active nests. The most abundant subcanopy nester, the Ovenbird (1-2 territorial males per ha), seldom used scolding calls when observers were near active nests, except 1 or 2 days before fledging. I anticipated that adults would reveal the general location of their nest, and the thermal imager would then be used to locate the nest itself. The next most abundant subcanopy nester, the Hermit Thrush, used scolding calls more frequently. However, I did not locate any Hermit Thrush nests with the device, and reasons for this are discussed below. If adult behavior does limit the usefulness of the device, then thermal imaging may be more useful with other species. For example, researchers studying grassland birds have had success in locating nests after flushing adults from their nests (S. Lima, pers. comm.).

Another possible explanation was the structure of nests. Although domes of some Ovenbird nests radiated heat, others were well-insulated and were only visible at the opening. Hermit Thrush nests lack domes, and only the adult itself or the nest cup radiated heat. Even though Hermit Thrush nests were usually visible from all sides, their overall heat signature was less obvious than that of Ovenbird nests. As a result, heat radiating from Hermit Thrush nests was often obscured by surrounding

vegetation.

A final explanation for the low success of the device in locating nests was the awkward thermal imaging interface. The camera has one eyepiece attached to the unit, and it was difficult to maintain a constant thermal view while moving through an area. A different thermal imaging interface could improve success in locating nests. In particular, a binocular fitting would enable the observer to have a constant infrared image of their surroundings and may increase the probability of detecting heat signatures of nests. Pursuing the design of such a device would be a fruitful avenue for further research.

Even though thermal imaging was not very useful for finding subcanopy nests, I did find two unexpected applications related to songbird breeding biology. First, the thermal imager was helpful in monitoring nests from distances up to 30 m, depending on the topography and vegetation density around the nest. For example, if the initiation date was known for a nest, then it was only necessary to determine that the nest was active during incubation. Thus, it was not necessary to approach the nest and disturb the adult during these checks. By minimizing disturbance during a nest check, bias in interpreting nest fates can be reduced (Martin and Geupel 1993). Thus, the thermal imager can be used to minimize bias resulting from observers monitoring nests.

Another unexpected application for the device was locating stationary fledglings. During the first week following fledging, young are unable to fly and lower their risk of predation by remaining still and silent (e.g. Anders et al. 1997). However, adults defend these young by using persistent scolding calls, and I was able to use these behavioral cues to locate young Nashville Warblers, Veeries and Ovenbirds after

scanning the defended area with the thermal imager. On these occasions, a stationary fledgling was located with the device from up to 30 m away. This is further evidence that adult behavior can enhance the usefulness of the device. More importantly, this demonstrates potential for the device to enhance studies on fledgling success of subcanopy nesters. Monitoring fledgling success of songbird territories may be important for determining the breeding productivity of species that have multiple nesting attempts per season. Despite my limited success at locating nests with the thermal imager, I assert that thermal imaging holds potential for further development for songbird observation applications.

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TABLE 1. Number of subcanopy nests found using traditional methods and a thermal imager in northern hardwoods of Aitkin County, Minnesota. Number of nests found using traditional methods were located while carrying thermal imager. Numbers in parentheses are nests found without flushing an adult from the nest.

Species	Number of nests found	
	Traditional methods	Thermal imager
Veery	1 (1)	0
Hermit Thrush	14 (8)	0
Red-eyed Vireo	4 (4)	0
Ovenbird	19 (16)	2
Indigo Bunting	1 (1)	0
Total	39 (30)	2