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EFFECTS OF SMALL FOREST OPENINGS ON THE BREEDING BIRD COMMUNITY IN A VERMONT HARDWOOD FOREST[1]

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Abstract. We examined the response of a forest bird community to the presence of small openings created by patch clear-cutting 0.4-ha plots within an extensive northern hardwood forest. We conducted bird censuses (June) and habitat measurements (July–August) in 102 census plots at four distances from openings in 1991 and 1992. Of 19 habitat variables measured, none differed significantly among forest plots at any distance from clear-cuts. Thirty-five (70%) of 50 bird species encountered during censusing were Neotropical migrants. Bird species richness did not differ as a function of distance from openings. However, species composition in plots within openings was least similar to that in plots farthest into forest, and most similar between the two distance categories farthest from openings. The movement of several forest-interior species away from openings, the addition of early-successional colonists in openings, and a high abundance of interior-edge species near openings contributed to the difference in species composition between openings and forest plots. As a group, Neotropical forest-interior migrants were significantly less abundant in openings than at any distance from them, and less abundant 50 m from openings than 200 m from them. Neotropical interior-edge migrants were significantly more abundant 50 m from openings than at any other distance. Nearctic migrants and nonmigrants did not respond to the presence of small openings. Of three locally common avian nest predators, none became more abundant in the openings. Brown-headed Cowbirds (*Molothrus ater*), also common locally, were never observed in or near the openings. Overall, bird species diversity increased in forested areas containing small openings due to the addition of edge and open-area nesters, but several forest-interior species were adversely affected by the presence of openings.

Key words: breeding birds, forest openings, patch clear-cuts, Neotropical migrants, Neartic migrants, Vermont.

INTRODUCTION

Managing habitats for high bird species diversity and abundance has become a task of utmost importance in light of recently documented declines in many Neotropical migrant bird species (Whitcomb et al. 1981, Ambuel and Temple 1982, Robbins et al. 1989a). Serious threats to populations of New World migrant birds exist on their North American breeding grounds in the form of habitat destruction, fragmentation, and loss of habitat diversity. Forest fragmentation increases the ratio of edge habitat to forest interior. Although edge habitat has been historically viewed as beneficial to a wide array of forest-dwelling wildlife (Leopold 1933), edge zones may contribute to reduced populations of bird species that require large areas of forest interior habitat (Gates and Gysel 1978, Ambuel and Temple 1983, Robinson 1992).

Many studies of edge effects have been conducted in highly fragmented regions and have identified fragment area as the most important factor explaining variation in the number of bird species present (Foreman et al. 1976, Blake and Karr 1984, 1987, Askins et al. 1990). Furthermore, small forest fragments contain species of Neotropical migrants in part because of immigration from nearby source populations (Askins and Philbrick 1987, Robinson 1992) and may be population sinks for many species (Robinson 1992, Donovan et al. 1995).

Neotropical forest-interior migrants in large forest tracts are not invulnerable to the effects of fragmentation (Coleman et al. 1982, Robbins et al. 1989b) or other disturbances, i. e., variation in post-timber harvest stand type or stand-

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level habitat characteristics (Hansen et al. 1995). In addition, some birds respond primarily to changes at the landscape scale, whereas others are influenced most by within-plot vegetation (Pearson 1993). Within regions of continuous forest, several studies have documented increases in bird species richness and density near edge zones created by adjacent land use types such as fields, power lines, clear cuts, or rivers (McElveen 1979, Strelke and Dickson 1980, Hansson 1983), whereas others have not noted such changes (Kroodsma 1982, Small and Hunter 1989).

Few studies have examined the effects of interior openings (those isolated in the interior of extensive forest regions), which represent early stages of fragmentation, on the breeding bird community of the surrounding forest. Thompson et al. (1992) compared populations of forest-interior migrants in an extensive mature hardwood forest between areas disturbed by recent clear-cutting and undisturbed forest. They found that while some species responded negatively to the presence of clear-cuts, others either showed no change, or reacted positively. Lent and Capen (1995) found that territory size influenced avian use of disturbed hardwood forest vegetation at different spatial scales, and reported the presence of several edge/open nesting species in forest openings as small as 0.7 ha. Keller and Anderson (1992) examined the effects of small clear-cuts on avian species composition and abundance in a coniferous forest. They determined that several bird species responded to the presence of preferred habitat types regardless of their proximity to forest interior edges. Most recently, Dellasala et al. (1966) inventoried breeding and wintering bird communities in the temperate rainforest of southeast Alaska. Small gaps (0.05 ha) created by felling trees in young forest (20 years old) influenced the distribution of 3 of the 16 species that bred there.

We examined the effect of small (0.4 ha) openings on the forest-interior bird community of an unfragmented northern hardwood forest. We tested for distance effects from openings by comparing similarity of species composition, species richness, and relative abundance of individual species and ecologically-related groups of species. These variables were compared within openings and at increasing distances from openings.

METHODS

STUDY AREA

Our study was conducted in 1990 and 1991 on the Rochester Ranger District of the Green Mountain National Forest (GMNF) in Vermont. The Green Mountain range is a series of steep ridges oriented north to south, which vary from 32 to 64 km wide and extend several hundred km from western Massachusetts north to southern Quebec. Within Vermont, the Green Mountains are one of six physiographic regions and comprise 7,252 km^2, 29% of the state's total area (Laughlin and Kibbe 1985). Regional elevations range from 300 to 1,330 m.

The Green Mountains are primarily northern hardwood forest, comprised of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*), with pockets of red spruce (*Picea rubra*) and balsam fir (*Abies balsamea*). Forest openings in this area include those created by timber harvesting, ski resorts, roads, and vacation home development (Laughlin and Kibbe 1985, DeGraaf and Rudis 1986). Our study sites spanned an area of 187.5 km^2, extending from 43°50′ to 44°07′ latitude and 72°51′ to 72°56′ longitude.

STUDY-SITE SELECTION

We selected five structurally and floristically similar study sites by researching GMNF timber harvest records and by field reconnaissance. Data were collected from 56 census plots during the summer of 1991, and from 46 plots in 1992, totaling 102 census plots located within the five sites. Twenty-eight plots were censused in both years. Our small forest openings were created by group selection timber harvesting (GSH). GSH creates a cluster of small clear-cuts (mean = 0.4 ha) within which $> 95\%$ of the trees have been removed. Standing forest was left between each opening (Fig. 1). On our sites, the forest separating the cuts ranged from 10 to > 100 m in width. The number of patches in a group selection cut ranged from < 10 to > 50, and the ratio of cleared area to forest within a timber sale boundary ranged from 20 to 36%. Study sites and census plots met the following criteria: (a) all sites were between 350 and 700 m elevation, (b) all sites were located in northern hardwood forest, (c) mature forest was adjacent to and surrounding all GSH sites, (d) GSH patches were

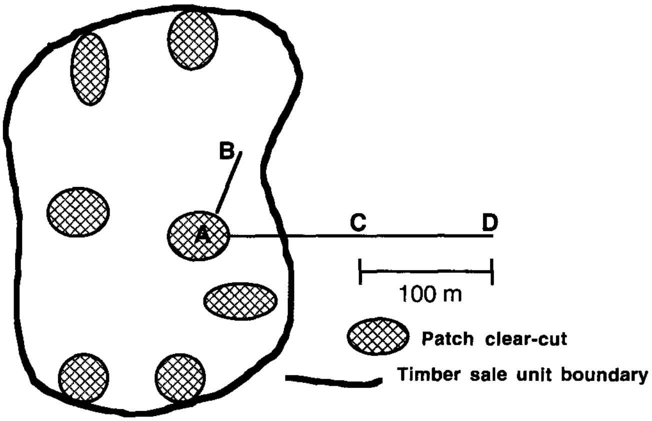

FIGURE 1. Patch cut openings (GSH sites), boundary, and census plot layout for a typical timber sale unit in the Green Mountain National Forest, Vermont. Letters denote bird census sites.

harvested between 1981 and 1990, (e) patches were approximately 0.4 ha in size, and (f) patch-opening density within GSH sites ranged from one patch per 0.9 ha to one patch per 1.3 ha.

All census plots were placed at one of four distances from openings. Twenty-five census plots were located at each of the following (Fig. 1): in the center of patch openings (A plots), 50 m into mature forest from the opening edge (B plots), 100 m into forest (C plots), and 200 m into forest (D plots). The five study sites were separated from each other by ≥ 5 km.

BIRD CENSUSING

We collected species presence data for forest birds in circular plots, 67 m in diameter, between 05:30 and 10:30 from 1 June through 3 July, 1991 and 1992. We chose plots of this size to exclude all edge vegetation in openings. We used circular census plots modified from the variable-width-circular-plot census method (Reynolds et al. 1980). We conducted each bird census by recording each individual detected within the plot during an 8-min period. Estimation of distances to singing birds was practiced on site for one week prior to actual censusing, and several plot boundaries at each site were flagged to ensure accuracy of distance estimates. All census plots were visited once per week for 4 weeks, with census routes changed during each survey to eliminate time-of-morning bias. Morrison et al. (1981) determined that avian density and species richness estimates stabilized at 4 visits/plot/season, using the Reynolds et al. (1980) circular plot census method.

We conducted censusing during the peak of the avian breeding season in the GMNF (Laughlin and Kibbe 1985, Morse 1989). During each census, an individual was considered present on a plot if it was detected by either aural or visual identification. To eliminate transient birds from our estimates of species richness and relative abundance, the frequency of occurrence for any bird species in any one census plot must have been ≥ 2 occurrences per 4 censuses (within one year). Morse (1989) states that the probability of detecting two transient individuals of the same species in the same census plot is low. Censusing was not conducted in rainy or windy weather.

HABITAT SAMPLING

We measured vegetation in 0.17-ha plots centered on the avian census plots using Noon's (1981) modifications of James' (1971) sampling technique. Nineteen habitat variables describing both abiotic and biotic attributes were measured on each plot. Percent live understory foliage was divided into three height classes: low (0–0.7 m), medium (0.7–1.5 m), and high (1.5–2.3 m). Shrubs were woody stemmed and < 3 cm diameter at breast height (dbh), and further categorized as small (< 3 m) or large (3–5 m), and as deciduous or coniferous. Counts of shrubs, *Rubus* spp., tree basal area, snags, and log volume were converted to number/ha.

DATA ANALYSES

Vegetation variables measured in plots within openings censused in both years were averaged because they were not independent. A matrix of vegetation plots and the 16 descriptors of vegetative attributes was subjected to cluster analysis to identify natural groupings of plots based on vegetative similarities. A hierarchical method was chosen using Pearson correlation and average linkage (Wilkinson 1990). We used Pearson correlation because it is not influenced by differences in scale between the objects used in the analysis.

We tested the resulting clusters for significant differences among the vegetative descriptors using a Mann-Whitney *U*-test (Zar 1984). We pooled vegetative data within each plot-distance category within forests (B, C, and D distance groups) and compared them for significant differences among all 19 habitat variables using a Kruskal-Wallis test (Zar 1984). Bonferroni tablewide significance level corrections were used where appropriate (Rice 1989). For these comparisons, we combined the number of small and large deciduous shrubs.

We compared similarity between the avian assemblage at each distance by the Bray-Curtis (1957) measurement using species composition and relative abundance measures as comparison criteria, where:

$$\text{similarity} = \left[\left(\sum 2\text{Wi}\right) \Big/ (\text{A} + \text{B})\right] \times 100\%$$

and: Wi = lower abundance of each species i present in both plots, A = number of individuals present in assemblage 1, and B = number of individuals present in assemblage 2.

Because all but five bird species in this study migrate annually to wintering grounds, some degree of evaluation (or re-evaluation) of breeding habitat by individuals must be done each season. Therefore, plots censused in both years were treated as independent plots for bird data analysis.

We used analysis of variance to test for differences in species richness and relative abundance among distances from openings. We normalized relative abundances for all species prior to analysis to adjust for landscape scale and population density differences among sites and between years. We normalized the data for each year by subtracting the mean relative abundance of each species at each site from that species' relative abundance at each distance in each site, after the method of Keller and Anderson (1992).

We defined *a priori* five groups of birds based on breeding habitat and migratory status. We assigned species to these groups based on similar classifications by Whitcomb et al. (1982) and Kendeigh (1982). We deviated from their classification, however, for two species, American Redstart and Magnolia Warbler, which we placed in the interior-edge group and the edge-open group, respectively, based on recent studies in New England (Thompson and Capen 1988, Small and Hunter 1989, Hunt 1996). Our groups were Neotropical forest-interior, interior-edge, and edge-open migrants, Nearctic migrants, and nonmigrants (see Table 2). A sixth group consisted of three species of Corvid nest predators. Because avian nest predators travel over a wide area, we considered Corvids present at any census plot in which they were detected at least once. We summed relative abundance for all species within each group to test for differences among distances. Tests for differences among distances also were performed on individual species within each group in the same manner in order to reveal species responses within the context of each ecological group. When considering ecological groups, we chose a significance level of $P < 0.05$; however, a significance level of $P < 0.10$ was considered significant when testing individual species. We did this to reduce the probability of a type II error, because erroneously rejecting the null hypothesis is more serious than a type I error when species conservation is being considered (Askins et al. 1990, Thompson et al. 1992). We used Tukey's multiple comparison tests in all instances where the null hypothesis of no change in abundance was rejected.

RESULTS

VEGETATION

Two distinct groups of plots were revealed by the cluster analysis. One cluster contained only openings and the other contained only forest plots. One B plot clustered by itself, so all data from this site were discarded. Both clusters contained a heterogeneous mixture of plots from each of the five sites. Within the forest cluster, plots were heterogeneously distributed among distance classes; i.e., no trend was apparent for plots from any particular site or distance to group together in either cluster.

No difference existed between the two plot-

TABLE 1. Habitat measurements for patch cut plots and forest plots based on cluster separation, Green Mountain National Forest, Vermont, 1991–1992.

Variable	Patch cuts[a] (n = 25)	Forest plots[a] (n = 54)	P[b]
Aspect	2.33 ± 0.26	2.17 ± 0.15	ns
Canopy closure (%)	25.39 ± 6.48	89.78 ± 1.24	<0.001
Canopy height (m)	2.82 ± 1.55	22.44 ± 0.53	<0.001
Coniferous basal area (m^2/ha)	0.31 ± 0.19	5.16 ± 1.42	0.041[c]
Coniferous dbh	4.42 ± 1.88	9.92 ± 1.73	ns
Deciduous basal area (m^2/ha)	2.81 ± 0.67	34.74 ± 1.16	<0.001
Deciduous dbh	19.55 ± 3.45	15.63 ± 0.50	ns
Elevation (m)	453.92 ± 86.07	453.75 ± 81.46	ns
Hi density board (%)	78.99 ± 5.62	48.68 ± 3.48	<0.001
Low density board (%)	98.36 ± 1.34	77.65 ± 2.90	<0.001
Live ground cover (%)	80.01 ± 3.06	43.37 ± 2.31	<0.001
Downed log volume (m^2/ha)	0.00 ± 0.00	190.34 ± 43.17	<0.001
Medium density board (%)	93.46 ± 2.49	45.89 ± 3.76	<0.001
# Coniferous shrubs	2.56 ± 2.27	89.96 ± 268.60	ns
# Deciduous shrubs	122.36 ± 131.34	853.96 ± 712.95	<0.001
# *Rubus* stems	158.75 ± 38.58	0.0 ± 0.0	<0.001
Slope	20.22 ± 2.01	19.00 ± 1.06	0.016[c]
# Snags	2.08 ± 0.29	11.56 ± 0.91	<0.001

[a] Mean ± SE.
[b] Mann-Whitney U-test.
[c] Not significant in sequential Bonferroni test.

clusters for slope, elevation, aspect, deciduous dbh, coniferous tree basal area, coniferous dbh, or number of coniferous shrubs (for patches, the latter four variables describe the $\leq 5\%$ trees remaining, Table 1). Significant differences did exist between the two clusters for variables describing both live understory and live ground cover (live ground cover, low, medium, and high understory foliage cover, number deciduous shrubs, and number *Rubus* sp. stems), and variables describing mature forests (log volume/ha, snags, deciduous tree basal area/ha, canopy closure, and canopy height). No significant difference existed for any variable when forest plots were pooled and compared among distances from openings.

BIRDS

Fifty species of birds were encountered during the two census seasons. Of these, breeding individuals of 36 species (72%) occurred on census plots in one or both years of the study. Three other species were avian nest predators: American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), and Blue Jay (*Cyanocitta cristata*).

In both years, Red-eyed Vireos (*Vireo olivaceus*), Ovenbirds (*Seiurus aurocapillus*), and Black-throated Blue Warblers (*Dendroica caerulescens*) were the most abundant species. These species comprised 14.1%, 12.9%, and 11.2%, respectively, of the total number of birds, accounting for 38.2% of all birds detected in the study. Ten of the 50 species censused were rare throughout the study area and were detected in census plots in only one year.

EFFECTS OF OPENINGS ON BIRDS

Twenty-seven species of birds were encountered within openings (A plots), whereas 24 species were found within plots at each of the three forest plot distances (B, C, D plots). This difference was not significant between any distance classes ($F_{3,32} = 0.5$, $P = 0.67$). Three species, Chestnut-sided Warblers (*Dendroica pensylvanica*), Common Yellowthroats (*Geothlypis trichas*), and Ruby-throated Hummingbirds (*Archilochus colubris*), were found only within openings, and several other species showed strong preferences for openings. Conversely, Black-throated Green Warblers (*Dendroica virens*), Brown Creepers (*Certhia americana*), Hermit Thrushes (*Catharus guttatus*), Solitary Vireos (*Vireo solitarius*), and Winter Wrens (*Troglodytes troglodytes*) never were encountered within openings. The remaining species were found in both forest and opening plots (Table 2).

Bray-Curtis similarity was low between openings and forest plots at all distances (Table 3). The highest coefficient of similarity in both

TABLE 2. Mean relative abundance of birds in patch cuts and three distances into the forest, Green Mountain National Forest, Vermont, 1991–1992.

Group/species	Distance from patch cut (m) 0	50	100	200	P^a
Neotropical edge-open migrants	0.379	0.055	0.103	0.064	<0.001
American Robin	0.018	0.030	0.091	0.037	<0.004
Cedar Waxwing	0.000	0.006	0.000	0.000	na
Chestnut-sided Warbler	0.146	0.009	0.000	0.000	<0.001
Common Yellowthroat	0.024	0.000	0.000	0.000	0.028
Least Flycatcher	0.009	0.004	0.012	0.027	ns
Magnolia Warbler	0.014	0.000	0.000	0.000	na
Mourning Warbler	0.110	0.006	0.000	0.000	<0.001
Ruby-throated Hummingbird	0.058	0.000	0.000	0.000	<0.001
Neotropical interior-edge migrants	0.222	0.360	0.215	0.237	0.001
American Redstart	0.060	0.073	0.034	0.051	ns
Eastern Wood-pewee	0.005	0.000	0.000	0.000	na
Great Crested Flycatcher	0.000	0.006	0.000	0.000	na
Red-eyed Vireo	0.072	0.186	0.176	0.171	0.005
Rose-breasted Grosbeak	0.078	0.033	0.000	0.009	0.001
Wood Thrush	0.007	0.062	0.005	0.006	0.029
Neotropical forest-interior migrants	0.219	0.398	0.494	0.532	<0.001
Black-and-white Warbler	0.044	0.022	0.020	0.013	ns
Blackburnian Warbler	0.007	0.006	0.009	0.013	ns
Black-throated Blue Warbler	0.058	0.173	0.099	0.095	0.019
Black-throated Green Warbler	0.000	0.011	0.083	0.143	<0.001
Canada Warbler	0.014	0.000	0.000	0.003	na
Hermit Thrush	0.000	0.000	0.005	0.016	0.023
Ovenbird	0.042	0.121	0.204	0.175	<0.001
Scarlet Tanager	0.005	0.013	0.035	0.016	ns
Solitary Vireo	0.000	0.000	0.000	0.024	0.044
Veery	0.049	0.052	0.039	0.034	ns
Nearctic migrants	0.125	0.165	0.131	0.128	ns
Brown Creeper	0.000	0.028	0.054	0.023	0.060
Golden-crowned Kinglet	0.000	0.000	0.000	0.000	na
Dark-eyed Junco	0.023	0.019	0.012	0.014	ns
Winter Wren	0.000	0.050	0.019	0.023	ns
White-throated Sparrow	0.053	0.009	0.019	0.000	0.060
Yellow-bellied Sapsucker	0.037	0.030	0.022	0.056	ns
Yellow-rumped Warbler	0.000	0.000	0.000	0.000	na
Nonmigrants	0.035	0.025	0.055	0.026	ns
Black-capped Chickadee	0.025	0.025	0.037	0.026	ns
Downy Woodpecker	0.005	0.000	0.006	0.000	na
Hairy Woodpecker	0.006	0.000	0.000	0.000	na
Pileated Woodpecker	0.000	0.000	0.006	0.000	na
White-breasted Nuthatch	0.000	0.000	0.005	0.000	na

[a] P values are for ANOVA, na = not abundant enough to test. Underlined values were not significant in Tukey's test.

TABLE 3. Percent similarity within the bird community in patch cuts and forest plots, Green Mountain National Forest, Vermont, 1991–1992.

	Distance (m) from patch cut			
	0	50	100	200
50	0.570	—		
100	0.463	0.723	—	
200	0.479	0.740	0.792	—

years (79%) was between plots 100 m and 200 m into the forest. In both years plots within openings were least similar to plots located 100 m into the forest (46%).

Relative abundance changed significantly among distances from openings for all three Neotropical migrant groups, but not for Nearctic migrants or nonmigrants (Fig. 2). Eight species of birds were Neotropical edge-open migrants that colonize early successional stage habitats or edge zones. This group displayed a highly significant distance effect ($F_{3,32}$ = 29.5, $P < 0.001$). A Tukey multiple comparison indicated that as a group they were significantly less abundant at all distances into the forest from openings. Chestnut-sided Warblers, Common Yellowthroats, Ruby-throated Hummingbirds, and Mourning Warblers (*Oporornis philadelphia*) were significantly less abundant in all forest plots than in openings (Table 2). American Robins (*Turdus migratorius*) were significantly more abundant in 100 m plots than in any other plots. Least Flycatchers (*Empidonax minimus*) displayed no significant trends among any distances. Although not abundant enough to test, Magnolia Warblers (*Dendroica magnolia*) occurred only in openings.

Six species were Neotropical interior-edge migrants. As a group, they also demonstrated a highly significant distance effect ($F_{3,32}$ = 7.1, P < 0.001). A Tukey multiple comparison indicated that they were significantly more abundant 50 m from openings than at all other distances, and that group abundance did not differ among any of the other distance classes. Three species demonstrated significant responses over distance from openings: Red-eyed Vireos were less abundant in openings, Wood Thrushes (*Hylocichla mustelina*) peaked in abundance in 50 m plots, but displayed no differences among other distances, and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) were more abundant in openings than in any forest plots (Table 2).

Ten species were Neotropical forest-interior migrants. This group also showed a highly significant distance effect ($F_{3,32}$ = 18.5, $P < 0.001$). A Tukey multiple comparison revealed significantly higher abundances in all forest plots than in openings, and significantly lower abundance in 50 m plots than in 200 m plots. Five species in this group reacted significantly to distance from openings. Hermit Thrushes were most abundant in 200 m plots, and Solitary Vireos were encountered only in 200 m plots. Oven-

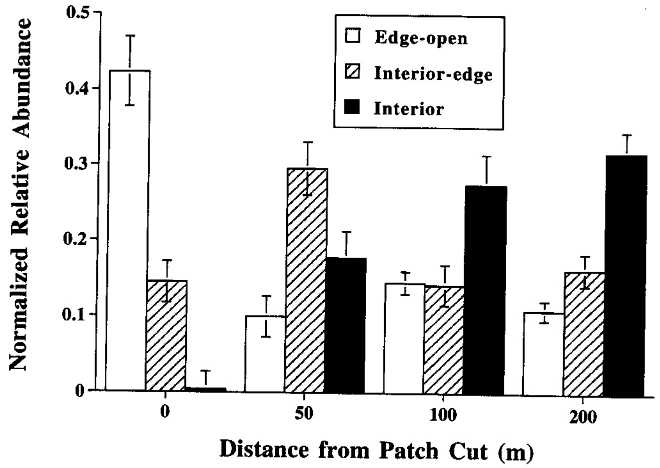

FIGURE 2. Normalized relative abundances as a function of distance from patch cuts for three groups of Neotropical migrant bird species in the Green Mountain National Forest, Vermont, 1991–1992 (mean + 0.2 ± SE).

birds and Black-throated Green Warblers were significantly less abundant in both openings and 50 m plots. Black-throated Blue Warblers peaked in abundance in 50 m plots and did not differ among the other distances.

In openings, Neotropical interior-edge migrants were significantly more abundant than Neotropical forest-interior migrants, and both were significantly less abundant than Neotropical edge-open migrants ($F_{2,24} = 41.4$, $P < 0.001$). Neotropical interior-edge migrants peaked in abundance at 50 m into forests, where they were significantly more abundant than both other Neotropical groups ($F_{2,24} = 8.9$, $P < 0.002$). Neotropical forest-interior migrants were significantly more abundant than both Neotropical edge-open migrants and Neotropical interior-edge migrants in both 100 m plots ($F_{2,24} = 6.7$, $P < 0.006$) and 200 m plots ($F_{2,24} = 25.7$, $P < 0.001$).

Eight species of birds were Nearctic migrants. This group showed no significant change in relative abundance among any plot distances ($F_{3,32} = 0.4$, $P = 0.78$). One species, Brown Creeper (*Certhia americana*), displayed a significant peak in abundance in 100 m plots.

The group of nonmigrants contained five species of birds. Abundance in this group did not differ among distances ($F_{3,32} = 0.9$, $P = 0.45$). Black-capped Chickadee (*Parus atricapillus*) was the only abundant member, and it displayed no change in abundance over distance.

American Crows and Common Ravens often were seen flying above plots and nearby forest areas, but were so rare within census plots that their abundances were pooled with those of the Blue Jay and termed "Corvids." Corvids showed no change in abundance between distances ($F_{3,32} = 0.7$, $P = 0.55$). Brown-headed Cowbirds (*Molothrus ater*) were never detected at any site, but were consistently present on nearby farms.

DISCUSSION

Small openings affect the forest-interior bird community in several ways. Wiens (1994) stated that forest fragmentation affects community dynamics through external factors that vary as the mosaic structure changes. The presence of small openings in our study area raised the overall community diversity through the addition of several species of early successional colonists, many of which were Neotropical migrants. Bird species richness was unchanged between openings and all forest plots. However, the Bray-Curtis similarity index reflected a turnover in bird species abundances as distance increased from openings: the decrease in numbers of forest-interior species near openings was offset by the addition of edge-open and interior-edge species. Small and Hunter (1989) similarly found bird species richness higher near powerlines than farther into forest habitat. Several edge-open species that were using the forest-powerline ecotone contributed to this difference. Our community similarity indices were similar to those of Keller and Anderson (1992), who found a 78% similarity between forest plots in fragmented versus unfragmented habitats near group selection harvest and stripcut sites.

We grouped Neotropical migrants according to their habitat associations in highly fragmented areas to examine their responses to openings in areas where fragment size was not a factor. Several species demonstrated responses inconsistent with their *a priori* groupings. American Robins, birds of open areas (Whitcomb et al. 1981) and insensitive to fragmentation (Temple 1986), were most abundant well away from openings. Several forest-interior birds did not retreat from the forest interior openings. We suggest that these species are affected by factors associated with greater degrees of fragmentation than present in our study, such as nest predation/parasitism or fragment size, but not by the presence of openings. Alternatively, the retreat of Black-throated Green Warblers, Hermit Thrushes, Ovenbirds, and Solitary Vireos from the openings demonstrates an aversion to even small proportions of forest edge, regardless of forest size.

The significant interaction between the Neotropical interior-edge and forest-interior birds across distance from openings could be a result of displacement near openings. Members of both groups are largely insectivorous, but the interior-edge species are well adapted to foraging in disturbed areas and edge zones where they may be outcompeting forest-interior birds.

Increased nest predation and egg parasitism near edges also have been suggested as causes of decreased abundances of forest-interior migrants (Wilcove 1985, Yahner and Cypher 1987, Yahner et al. 1993). Six of the 10 Neotropical forest-interior birds were species that nest on or within 0.3 m of the ground, whereas none of the Neotropical interior-edge species nest there

(Bent 1963, 1964, DeGraaf and Rudis 1986). Wilcove (1985) found that artificial ground nests were disturbed more often than nests placed 1.5 m above ground. However, Yahner and Scott (1988) found that artificial nests placed on the ground were preyed upon less often than nests placed 1.5 m above the ground when birds were the primary predators. We found no increase in abundance of Blue Jays, Crows, or Ravens near openings, and no Brown-headed Cowbirds at any site, indicating that avian nest predation and egg parasitism were not factors affecting nesting success around small forest openings. This may be because the edges of small openings are discontinuous and not as easily detectable or exploitable as are edges of large openings, although there is more total edge in several small openings than in one large opening of equal total size.

Most members of the nonmigrant and Nearctic migrant groups were rare. Populations of short-distance and nonmigrant birds are less affected by habitat fragmentation than are Neotropical migrant songbirds (Galli et al. 1976, Crawford et al. 1981). Four of the five nonmigrant species we censused forage on tree trunks, and all five nest in tree cavities, usually in snags. Although there were fewer snags standing in openings than forest plots, some snags were left in each opening to benefit wildlife. We observed Black-capped Chickadees nesting in several of these. Depredation rates are low in tree cavity nests (Wilcove 1985), which may allow cavity nesting species to select nest sites based on microhabitat criteria alone, thus broadening the range of acceptable nesting habitats for them. Only one of the Neotropical migrants present in this study nests in tree cavities (Great-crested Flycatcher); it was extremely rare in this study. Tree trunks were exploited as feeding substrates by only one Neotropical migrant (Black-and-white Warbler) and snags were unexploited by Neotropical migrant birds except as perch sites. Only one member of the Nearctic migrant group, the Brown Creeper, was significantly less abundant near openings than in deeper forest. Keller and Anderson (1992) found a similar response exhibited by this species in plots in fragmented and unfragmented forest areas.

Group selection harvesting is an appropriate harvest method in areas containing sensitive or declining forest-interior species that are known to suffer from cowbird parasitism or predation from Corvids. Group selection harvest sites were less visible in the landscape than other clear-cut methods, due to the smaller openings scattered within the remaining tree canopy. Six of the seven species showing significant declines in abundance near patch cuts were Neotropical migrants, five of which were forest-interior birds. Some Neotropical migrant forest-interior birds displayed sensitivity to the creation of edges within large forest interiors, indicating that they are limited by edge zones rather than forest fragment size. Others did not respond to interior openings, indicating that factors limiting their abundance were more complex than the mere presence of edges.

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LITERATURE CITED

AMBUEL, B., AND S. A. TEMPLE. 1982. Songbird populations in southern Wisconsin forests: 1954 and 1979. J. Field Ornithol. 53:149–158.

AMBUEL, B., AND S. A. TEMPLE. 1983. Area-dependent changes in bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. Current Ornithol. 7:1–57.

ASKINS, R. A., AND M. J. PHILBRICK. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. Wilson Bull. 99:7–21.

BENT, A. C. 1963. Life histories of North American wood warblers. Dover Publications, New York.

BENT, A. C. 1964. Life histories of North American thrushes, kinglets, and their allies. Dover Publications, New York.

BLAKE, J. G., AND J. R. KARR. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. Biol. Conserv. 30:173–187.

BLAKE, J. G., AND J. R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724–1734.

BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

COLEMAN, B. D., M. A. MARES, M. R. WILLIG, AND Y. HSIEH. 1982. Randomness, area, and species richness. Ecology 63:1121–1133.

CRAWFORD, H. S., R. G. HOOPER, AND R. W. TITTERINGTON. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. J. Wildl. Manage. 45:680–692.

DEGRAAF, R. M., AND D. D. RUDIS. 1986. New England wildlife: habitat, natural history, and distribution. U.S.D.A. For. Serv. Gen. Tech. Rep. NE-108.

DELLASALA, D. A., J. C. HAGAR, K. A. ENGEL, W. C. MCCOMB, R. L. FAIRBANKS, AND E. G. CAMPBELL. 1966. Effects of silvicultural modifications of temperate rainforest on breeding and wintering bird communities, Prince of Wales Island, southeast Alaska. Condor 98:706-721.

DONOVAN, T. M., F. R. THOMPSON, III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in sources and sinks. Conserv. Biol. 9:1380–1395.

FOREMAN, R. T., A. E. GALLI, AND C. F. LECK. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia 26:1–8.

GALLI, A. E., C. F. LECK, AND R. T. FOREMAN. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356–364.

GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59:871–883.

HANSEN, A. J., W. C. MCCOMB, R. VEGA, M. G. RAPHAEL, AND M. HUNTER. 1995. Bird habitat relationships in natural and managed forests in the west cascades of Oregon. Ecol. Applic. 5:555–569.

HANSSON, L. 1983. Bird numbers across edges between mature conifer forest and clearcuts in central Sweden. Ornis Scand. 14:97–103.

HUNT, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. Auk 113:875–888.

JAMES, F. C. 1971. Ordination of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

KELLER, M. E., AND S. A. ANDERSON. 1992. Avian use of habitat configurations created by forest cutting in southeastern Wyoming. Condor 94:55–65.

KENDEIGH, S. C. 1982. Bird populations in east central Illinois: fluctuations, variations, and development over a half-century. Ill. Biol. Monogr. 152:1–136.

KROODSMA, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. J. Appl. Ecol. 19:361–370.

LAUGHLIN, S. B., AND D. P. KIBBE [eds.]. 1985. The atlas of breeding birds of Vermont. Univ. Press of New England, Hanover, MA.

LENT, R. A., AND D. E. CAPEN. 1995. Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest. Ecography 18:97–108.

LEOPOLD, A. 1933. Game management. Scribners, New York.

MCELVEEN, J. D. 1979. The edge effect on a forest bird community in North Florida. Proc. Annu. Conf. Southeastern Assoc. Fish and Wildl. Agency 31:212–215.

MORRISON, M. L., R. W. MANNAN, AND G. L. DORSEY. 1981. Effects of number of circular plots on estimates of avian density and species richness. Stud. Avian Biol. 6:405–408.

MORSE, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, MA.

NOON, B. R. 1981. Techniques for sampling avian habitats, p. 42–52. *In* D. E. Capen [ed.], The use of multivariate statistics in studies of wildlife habitat. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-87.

PEARSON, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. 8:3–18.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROBBINS, C. S., C. D. DAWSON, AND B. DOWELL. 1989b. Habitat area requirements of breeding forest birds of the Mid-Atlantic states. Wildlife Monogr. 103:1–34.

ROBBINS, C. S., J. R. SAUER, AND R. GREENBERG. 1989a. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86:7658–7662.

ROBINSON, S. K. 1992. Population dynamics of breeding birds in a fragmented Illinois landscape, p. 408–418. *In* J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

SMALL, M. F., AND M. L. HUNTER, JR. 1989. Response of passerines to abrupt forest-river and forest-powerline edges in Maine. Wilson Bull. 101:77–83.

STRELKE, W. K., AND J. G. DICKSON. 1980. Effect of forest clear-cut edge on breeding birds in east Texas. J. Wildl. Manage. 44:559–567.

TEMPLE, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models, p. 301–304. *In* J. Verner, M. L. Morrison, and C. J. Ralph [eds.], Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI.

THOMPSON, F. R., III, AND D. E. CAPEN. 1988. Avian assemblages in seral stages of a Vermont forest. J. Wildl. Manage. 52:771–777.

THOMPSON, F. R., III, W. D. DIJAK, T. G. KULOWIEC, AND D. A. HAMILTON. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. J. Wildl. Manage. 56:23–30.

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, p. 125–205. *In* R. L. Burgess and D. M. Sharpe [eds.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

WIENS, J. A. 1994. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis 137:s97–s104.

WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

WILKINSON, L. 1990. SYSTAT: the system for statistics. Systat, Inc., Evanston, IL.

YAHNER, R. H., AND B. L. CYPHER. 1987. Effects of nest location on depredation of artificial arboreal nests. J. Wildl. Manage. 51:178–181.

YAHNER, R. H., C. G. MAHAN, AND C. A. DELONG. 1993. Dynamics of depredation on artificial ground nests in habitat managed for Ruffed Grouse. Wilson Bull. 105:172–179.

YAHNER, R. H., AND D. P. SCOTT. 1988. Effects of forest fragmentation on depredation of artificial nests. J. Wildl. Manage. 52:158–161.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.