Roads as Edges: Effects on Birds in Forested Landscapes

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ABSTRACT. Numerous studies have documented that forest edges affect habitat use and reproductive success of forest birds, but few studies have considered edges created by narrow breaks in the forest canopy. We compared predation rates on artificial nests placed within forest habitat along edge transects, 10 m from unpaved roads, and along interior transects, 300 m from forest-road boundaries. Local factors, such as nest concealment, and landscape factors, such as the degree of forestation in surrounding areas, were accounted for when testing for edge effects on nest predation. We conducted fixed-radius point counts to compare relative abundance of 34 bird species on edge and interior transects. Also, seven study plots were established adjacent to unpaved roads to map the distribution of bird territories within edge areas, 0–150 m from unpaved roads, and interior areas, 150–300 m from roads. Rates of nest predation on artificial nests did not differ between edge and interior transects, but the distribution of forest birds was influenced by unpaved roads. Four of 18 forest-interior species had lower relative abundance or territory density adjacent to roads, while four of six species categorized as edge nesters had higher relative abundance on edge transects. Our results suggest that narrow openings within forested landscapes may affect habitat use but not nest predation levels, emphasizing the need to frame definitions of "edge effects" within the context of multiple ecological processes. For. Sci. 48(2):381–390,

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Reported declines in forest bird populations may be related to fragmentation of breeding habitat in North America (Robinson et al. 1995). Studies in avian ecology have identified a set of area-sensitive species whose richness and density decrease as forest size decreases, and forest edges are frequently implicated for this pattern (Askins et al. 1990, Paton 1994). Most area-sensitive species are also classified as forest-interior species, defined to "rarely" nest near edges (Whitcomb et al. 1981, Freemark and Collins 1992). Elevated levels of nest predation and cowbird parasitism and decreased levels of pairing and nesting success have been documented adjacent to forest-nonforest interfaces and in forest fragments (Paton 1994, Robinson et al. 1995, Van Horn et al. 1995). However, most studies examining effects of forest fragmentation on birds have focused on juxtapositions of forest with extensive openings such as fields or clearcuts, disregarding narrow breaks in the forest canopy such as roads (Paton 1994, Rich et al. 1994).

Rich et al. (1994) studied forest bird abundance relative to narrow openings in a heavily forested landscape, recording lower abundance of area-sensitive birds along powerline corridors (23-m-wide) and paved roads (16-m-wide) but not along unpaved roads (8-m-wide). They reported that decreased abundance at edge points resulted from the absence of forest habitat within the openings, which reduced the forest area within survey-point radii. Similarly, King et al. (1997) described how reduced densities of forest-interior species near edges could result from "passive displacement" of territory centers, occurring if birds limit their territories entirely to forest habitat. However, in various studies involv-

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ing wide openings (>25 m), others have suggested that reduced densities near edges reflect differential habitat structure, decreased resource levels, increased competition from edge species, or diminished reproductive success (Strelke and Dickson 1980, Ambuel and Temple 1983, Villard et al. 1993, Van Horn et al. 1995). Differences in habitat quality may thus cause active avoidance of edge areas (Kroodsma 1984, Villard et al. 1993, Van Horn et al. 1995).

Nest predation has been characterized as the primary source of nest mortality for open-nesting passerine birds (Martin 1992). Of numerous published studies of nest predation, we know of only two that examined predation levels relative to road edges. Although Yahner and Mahan (1997) reported no difference in nest predation rates near and far from unpaved logging roads, the treatment designed to test for a road-edge effect was confounded by proximity to clearcut edges for 64 of 89 artificial nests. Lindenmayer et al. (1999) found no pattern in artificial nest predation relative to gravel roads within an Australian plantation of non-native pines, but applicability of these results to other landscapes may be limited. As described for other types of edges (Bider 1968, Chasko and Gates 1982, King et al. 1998), vegetation structure of forest-road borders may concentrate activity of nest predators. Researchers have also suggested specific associations between roads and nest predators (Small and Hunter 1988, Askins 1994, Paton 1994).

We studied the effects of unpaved roads on forest birds in an extensively forested region. To examine the distribution of forest birds relative to roads in more detail than reported by Rich et al. (1994), we considered relative abundance, territory placement, and vegetation structure. In addition, we tested whether predation levels of artificial nests were elevated adjacent to roads, considering both local and landscape-scale habitat factors.

Study Area

The 370 km^2 study area spanned portions of the Middlebury and Rochester districts of the Green Mountain National Forest in Vermont. Forest comprised 94% of the region, while the remaining area consisted of young, regenerating forest (<9 yr old); undeveloped openings such as hayfields and maintained wildlife openings; wetlands and open water; and developed openings including ski areas, residential areas, and dairy operations. Roads, of which 70% were unpaved, traversed the region at an average density of 700 m/km^2.

Northern hardwood forests dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) comprised 82% of the forested area in the region. The remaining forest consisted of mixed northern hardwood/red spruce (*Picea rubens*)–balsam fir (*Abies balsamea*) stands, and conifer stands comprised primarily of high-elevation spruce and fir. Other overstory species included white ash (*Fraxinus americana*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), eastern hemlock (*Tsuga canadensis*), and eastern white pine (*Pinus strobus*).

Methods

Establishment of Study Sites

We used a geographic information system (GIS) and current GIS coverage of forest stands, forest openings, and roads to select study sites along unpaved roads bisecting contiguous forest. Gravel and dirt roads were divided into 200 m segments, and segments with forested area extending 300 m from the road and at least 100 m from other openings were identified. From this set, we randomly selected 25 nonadjacent study sites, rejecting segments not located within northern hardwood or mixed northern hardwood/spruce–fir stands. Selected road segments averaged 9.6 ± SE of 0.71 m in width (between forest canopies) and were located at elevations of 400–690 m.

At each site, we established two 200 m transects for use in artificial nest experiments and point-count surveys conducted in our first field season. Transects were parallel to the road and located at the "edge," 10 m from the forest-road border; and in the "interior," 300 m from the forest border. Distance to nearest opening did not differ ($F_{1,48} = 2.62$, $P > 0.1$) between edge transects ($x = 246.7 \pm 25.49$ m, range 104.8 to 576.9 m) and interior transects ($x = 313.0 \pm 32.15$ m, range 106.1 to 652.5 m). Transects 300 m from the border should be representative of interior forest as most studies indicate that edge effects on predation are concentrated within 50 m of forest borders (Paton 1994). Similarly, studies examining edge effects on bird distribution generally compare areas adjacent to forest borders to those >150 m away (Wenny et al. 1993, Rich et al. 1994, King et al. 1997).

During a second field season, we established census plots at seven of our study sites to further examine the distribution of bird territories relative to roads. Sites were selected for their general uniformity of management history and forest composition and were located in northern hardwood forest >50 yr in age. Each census plot, marked in a 25 m grid, began at the road and extended 300 m into the forest. Six plots were 300 m long and one was 250 m long, yielding six 9 ha plots and one 7.5 ha plot. For analyses, "edge areas," 0–150 m from roads, were compared to "interior areas," 150–300 m from roads. We selected 150 m distance classes because they were wide enough to encompass bird territories and relevant to comparisons made in other edge-related studies of bird distribution. Distance to nearest opening did not differ between edge areas and interior areas (Ortega and Capen 1999).

Artificial Nest Protocol

We used artificial nests to index predation rates on edge and interior transects. Although artificial nests do not necessarily provide an accurate estimate of depredation rates at real nests (e.g., Sloan et al. 1998), they are widely used to address comparative questions and may provide a valid index of predation intensity (Reitsma et al. 1990, Paton 1994). We used two types of nests because predation levels on birds' nests are influenced by nest height, and many studies have obtained differing results for nests placed on the ground versus above ground (e.g., Martin 1987, Rudnicky and Hunter 1993). Our "shrub" nests were commercial canary wicker baskets (9.5 cm wide × 3.5 cm

deep) that we lined with vegetation collected on site and placed in shrubs 1–2 m above the ground. "Ground" nests consisted of depressions formed in the ground at the bases of plants.

Eight nests were established at 25 m intervals along each transect, and ground nests were alternated with shrub nests. Each nest was baited with two Japanese quail (*Coturnix coturnix*) eggs and placed 5 m from the transect line at a randomly selected compass bearing. All nests were positioned to reduce visual exposure to predators (Martin 1992). To control for differential nest exposure, we measured concealment of each nest after completion of predation experiments (see *Local Habitat Measurements*). Precautions were taken to minimize human scent on eggs, nests, and transects (Rudnicky and Hunter 1993).

Nests were exposed for seven nights, after which overturned nests and those with missing, cracked, or crushed eggs were recorded as depredated (Rudnicky and Hunter 1993, Paton 1994). The experiment was conducted twice at each site (June 2 – July 2, 1995), and timed to correspond to the typical period of songbird egg-laying and brood-rearing in the region. During the second trial, the sequence of ground and shrub nests along the transects was opposite to that used in the first trial. We calculated predation rates as the proportion of nests depredated per trial for each transect and type of nest.

Point Count Protocol

We used 10 min., fixed-radius point counts (Ralph et al. 1993) to index the abundance of forest birds along nest transects from May 30 through July 2, 1995. Counts were conducted within 4 hr of sunrise and never while artificial nests were present on transects. Each transect was surveyed at three points spaced at 100 m intervals, and birds seen or heard within 50 m of each point were recorded. We also recorded detections of eastern chipmunks (*Tamias striatus*) and red squirrels (*Tamiasciurius hudsonicus*) because studies have shown that squirrels and chipmunks, along with blue jays (*Cyanocitta cristata*), are often the most important nest predators in forested landscapes (Chasko and Gates 1982, Paton 1994, Hanski et al. 1996).

To minimize observer and temporal effects, each transect was surveyed twice, once by each of two observers and once during each half of the morning survey period. For each species on each transect, the higher number of detections of the two surveys was used as the estimate of relative abundance. We used published classifications (Whitcomb et al. 1981, Freemark and Collins 1992) to group species by their defined tendency to nest near edges (edge species), away from edges (forest-interior species), or within both types of habitat (interior-edge species). Estimates of relative abundance per transect were calculated for each edge-use group. Species detected on <10% of transects were not included in analyses, and one edge transect was eliminated because of proximity to a stream.

Territory Mapping

From May 31 through June 29, 1996, we used the spot-mapping technique to delineate territories of male birds on census plots (International Bird Census Committee 1970). Censuses were conducted within 5 hr of sunrise, during which all bird detections were recorded on grid maps. Observers walked systematically (4 ha/hr) along the center of each 50-m-wide strip parallel to the road. Detections outside of plot boundaries were recorded to improve mapping of boundary territories (Marchant 1981), and those of uncertain location were investigated further. Plots were assessed 10 times each, with visits spaced every 2–4 days. Territories were defined as clusters of three or more registrations from different visits, and adjacent clusters were delineated by countersinging events and simultaneous registrations (International Bird Census Committee 1970).

We assigned territories to distance classes according to the perpendicular distance between the center of the territory and the road. Densities were calculated as number of territory centers per 10 ha for edge and interior areas on each plot. Densities were also compared among 50 m distance intervals that extended from the road 300 m into the forest. Species with <10 mapped territories were excluded from analyses.

Local Habitat Measurements

To estimate nest concealment, we positioned a board with 50 (10 × 10 cm) black-and-white squares arranged in a 10 × 5 checkerboard pattern at each nest location, and viewed the board from a distance of 5 m in the four cardinal directions. The number of squares >50% covered by vegetation was determined for two height strata, 0–1 m above ground for ground nests and 1–2 m above ground for shrub nests (Leimgruber et al. 1994). Scores were averaged for each type of nest on each transect for use in analyses of transect predation rates.

To consider vegetation structure in relation to roads, we measured 13 variables considered important in characterizing forest bird habitat (Van Horn et al. 1995, King et al. 1997). In 1995, we centered a circular 0.04 ha plot on each avian survey point. Canopy cover and ground cover were estimated with a sighting tube at 40 equally spaced points along four 22.6 m transects oriented to the cardinal directions and crossing at plot center (James and Shugart 1970). We indexed shrub density by counting the number of stems [>1 m tall, <5 cm diameter at breast height (dbh)] within 1 m of these transects. Basal area was estimated using a 2.5 (m^2/ha)-factor prism. To consider tree species composition, we calculated relative densities (ratio of basal area to total basal area) of conifers and common deciduous species within vegetation plots. Diameter of trees included in the assessment of basal area was measured with a dbh tape and averaged for each vegetation plot. For analyses of predation rates, vegetation variables were averaged per transect.

In 1996, we measured habitat variables on our census plots. Circular, 0.04 ha plots were established systematically at 100 m intervals along the center gridline of each 50 m strip. Canopy cover, ground cover, basal area, tree species composition, and dbh were measured as described previously. In addition, at the center of each vegetation plot, we measured leaf litter depth and shrub height and used a clinometer to estimate slope and canopy height.

Landscape Variables

To consider the influence of landscape composition on predation rates of artificial nests, we derived landscape variables using a GIS. Proportions of both forest cover and developed land were calculated for the area defined by a 2-km-radius circle centered on each transect. We also considered landscape variables derived with a 5-km-radius circle to account for differing home range sizes among predator species (DeGraaf and Rudis 1986, Robinson et al. 1995). Landscape variables derived at scales broader than 5 km had low variability and were therefore not analyzed.

Statistical Analyses

We used ANOVA to test nest predation rates, relative abundance of birds and sciurids, territory density, and vegetation variables for differences between edge and interior classes (i.e., a "road proximity" effect). For comparisons between distance classes of census plots, site was included in the ANOVA model as a blocking factor (Sokal and Rolf 1981, p. 349–359) because plots had been selected for homogeneity and because territories frequently shared area between distance classes.

For examination of nest predation rates, nest type and the nest type–road proximity interaction were included as main effects in the general model. We added nest concealment and landscape variables to the model as covariates to test for their influence on nest predation rates. Before a variable was included as a covariate, we performed two tests to assess whether ANCOVA was appropriate: (1) the general model was used to assure that the variable was not influenced by the main effects, and (2) interactions between covariates and main effects were evaluated within the general model to address the equality of slopes requirement of ANCOVA (Tabachnick and Fidell 1989, p. 324). The "full model" used to test for covariate effects included main effects and variables satisfying the above requirements. Each set of landscape variables derived at a unique scale was tested separately, and the final model used to test main effects included only those covariates that were significant in the full-model tests.

We tested assumptions of normality and homogeneity of variance for all dependent variables with Shapiro-Wilk and F_{max} tests, and applied standard transformation methods where necessary (Tabachnick and Fidell 1989, p. 83–87). Variables that could not be successfully transformed were ranked and then tested as described previously. Statistical significance was set at $P < 0.1$ because statistical power at the $P = 0.05$ level was low (<0.4; Cohen 1988, p. 311–313) for individual-species tests of relative abundance and territory density.

Results

Local Habitat Variables in Relation to Roads

Of four vegetation variables characterizing forest structure at survey points on transects, only canopy cover differed between edge and interior classes (canopy cover: $F_{1,134} = 5.77$, $P = 0.018$; shrub density, dbh, and basal area: $F_{1,134} < 1.70$, $P > 0.19$), although the difference in means was small (edge: 63.4 ± 1.42%; interior: 58.2 ± 1.61%). Relative densities of sugar maple, red and striped maple (*Acer pensylvanicum*), American beech, yellow birch, and conifer species did not differ between edge and interior transect points ($P > 0.1$). For census plots, measurements of shrub density, dbh, basal area, and canopy cover showed no differences between edge and interior areas ($F_{1,106} < 0.84$, $P > 0.36$). Similarly, slope, litter depth, shrub height, canopy height, and relative densities of tree species did not differ between edge and interior areas ($P > 0.30$).

Nest Predation

We retrieved 739 of 800 artificial nests of which 303 (41%) were scored as depredated. Because predation rates could not be normalized, we used ranked values in all analyses. Predation rates did not differ between the two trial periods ($F_{1,192} = 0.43$, $P = 0.51$), and trial did not interact with other main effects ($F_{1,192} < 0.9$, $P > 0.3$ for all interactions). Therefore, predation rates calculated across the two trials were used in subsequent analyses.

Nest concealment and the four landscape variables satisfied requirements of ANCOVA. Nest concealment did not differ between edge and interior transects ($F_{1,99} < 0.01$, $P = 0.95$), was lower for ground nests versus shrub nests ($F_{1,99} = 3.62$, $P = 0.06$), but was not influenced by a road-proximity-by-nest type interaction ($F_{1,99} = 0.05$, $P = 0.82$). Landscape variables did not vary with road proximity ($F_{1,99} < 0.03$, $P > 0.89$).

In the full model with covariates, nest concealment did not influence predation rates ($F_{1,93} = 0.14$, $P = 0.71$). This result held when we tested each nest type separately ($F_{1,45} < 0.15$, $P > 0.7$ for both nest types). At the 2 km landscape scale, neither forest cover nor developed land was a significant covariate in explaining variation in nest predation rates ($F_{1,93} < 0.38$, $P > 0.54$). This result held for landscape variables generated at the 5 km scale ($F_{1,93} < 1.9$, $P > 0.17$).

We used a reduced model without covariates to test for effects of nest type and road proximity on nest predation rates. Predation rates did not differ between edge and interior transects ($F_{1,99} < 0.01$, $P > 0.9$; Figure 1). However, predation levels were higher for shrub nests compared to ground nests ($F_{1,99} = 94.16$, $P < 0.001$), and this pattern held across

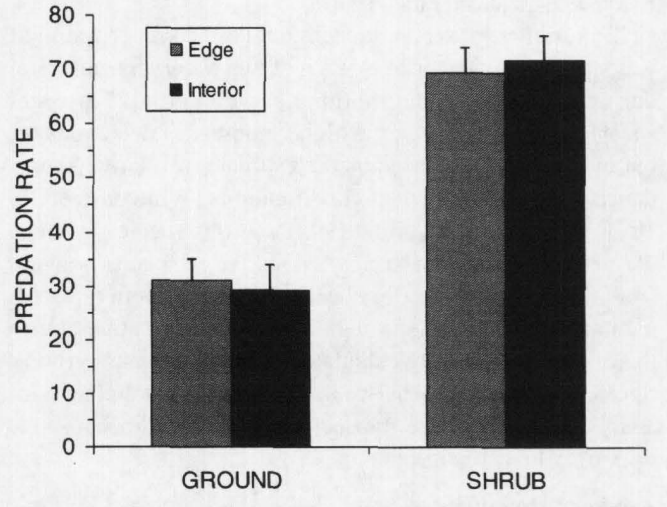

Figure 1. Mean (±SE) ranked nest predation rates on artificial ground and shrub nests for edge and interior transects on the Green Mountain National Forest, 1995.

edge and interior transects (nest-type-by-road-proximity interaction: $F_{1,99} = 0.23$, $P = 0.64$). Overall, the reduced model accounted for 50% of variation in nest predation rates ($R^2 = 0.50$, $P < 0.001$). For both shrub and ground nests, we found no relationship between predation rates and local habitat variables ($r < 0.2$). Of 113 detections of potential predators, 24% were of blue jays, 34% of red squirrels, and 42% of chipmunks. For all three predator species, relative abundance did not differ between edge and interior transects ($F_{1,47} < 2.40$, $P > 0.12$).

Bird Abundance and Distribution

Among 18 species classified as forest-interior nesters, winter wrens, hermit thrushes, and ovenbirds were less abundant on edge transects compared to interior transects in 1995, and American redstarts and black-and-white warblers showed the opposite pattern (Table 1). For forest-interior species as a group, relative abundance did not differ between edge and interior transects (Table 1). Among six edge species, American robins, cedar waxwings, chestnut-sided warblers, and dark-eyed juncos were more abundant on edge versus interior transects (Table 1). As a group, edge species had significantly higher relative abundance at edges (Table 1). None of 10 species classified in the interior-edge category had differences in relative abundance between edge and interior classes, and comparable results were obtained when interior-edge species were analyzed as a group (Table 1).

Five species had sufficient sample size of spot-mapped territories in 1996 to allow a more detailed examination of their distribution relative to roads. Two interior species, ovenbirds and black-throated green warblers, had lower territory densities within edge versus interior areas of census plots (Table 1). For these species, territory distribution over 50 m distance intervals showed a series of peaks and lows in density (Figure 2). Spot maps revealed that clustering of territory centers within certain distance

Table 1. Relative abundance of birds on 49 transects in 1995 and density of territories on 7 census plots in 1996, compared between edge and interior classes of study sites on the Green Mountain National Forest.

	Transects			Census plots		
	Rel. abun.	P*	Effect†	No. terrs††	P*	Effect†
Forest-interior species	931	0.971				
Hairy woodpecker (*Picoides villosus*)	18	0.931				
Red-breasted nuthatch (*Sitta canadensis*)	25	0.656				
White-breasted nuthatch (*S. carolinensis*)	29	0.891				
Brown creeper (*Certhia americana*)	25	0.753				
Winter wren (*Troglodytes troglodytes*)	20	0.085	I > E			
Golden-crowned kinglet (*Regulus satrapa*)	18	0.827				
Veery (*Catharus fuscescens*)	36	0.456				
Swainson's thrush (*C. ustulatus*)	22	0.154				
Hermit thrush (*C. guttatus*)	41	0.033	I > E			
Black-thr. blue warbler (*Dendroica caerulescens*)	162	0.481		36	0.135§	
Yellow-rumped warbler (*D. coronata*)	47	0.149				
Black-thr. green warbler (*D. virens*)	109	0.423		45	0.006§	I > E
Blackburnian warbler (*D. fusca*)	67	0.626				
Black-and-white warbler (*Mniotilta varia*)	19	0.071	E > I			
American redstart (*Setophaga ruticilla*)	68	0.017	E > I	27	0.006	E > I
Ovenbird (*Seiurus aurocapillus*)	176	0.095	I > E	49	0.015§	I > E
Canada warbler (*Wilsonia canadensis*)	21	0.270				
Scarlet tanager (*Piranga olivacea*)	28	0.386				
Edge species	185	0.002	E > I			
Least flycatcher (*Empidonax minimus*)	11	0.141				
American robin (*Turdus migratorius*)	78	0.002	E > I			
Cedar waxwing (*Bombycilla cedrorum*)	19	0.071	E > I			
Chestnut-sided warbler (*Dendroica pensylvanica*)	19	0.080	E > I			
White-throated sparrow (*Zonotrichia albicollis*)	9	0.227				
Dark-eyed junco (*Junco hyemalis*)	49	0.025	E > I			
Interior-edge species	459	0.177				
Ruffed grouse (*Bonasa umbellus*)	5	0.679				
Yellow-bellied sapsucker (*Sphyrapicus varius*)	54	0.310				
Downy woodpecker (*Picoides pubescens*)	6	0.385				
Northern flicker (*Colaptes auratus*)	7	0.185				
Blue-headed vireo (*Vireo solitarius*)	62	0.723				
Red-eyed vireo (*V. olivaceus*)	172	0.363		60	0.437§	
Blue jay	40	0.564				
Black-capped chickadee (*Poecile atricapilla*)	67	0.703				
Common yellowthroat (*Geothlypis trichas*)	10	0.134				
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	36	0.648				

* ANOVA of ranked data (unless otherwise indicated); df = 1 and 47 for transects, and df = 1 and 6 for census plots.
† For species with significant differences between edge (E) and interior (I) classes ($P < 0.1$), the relative magnitude of the effect is indicated.
†† Blanks indicate insufficient data.
§ ANOVA of unranked data.

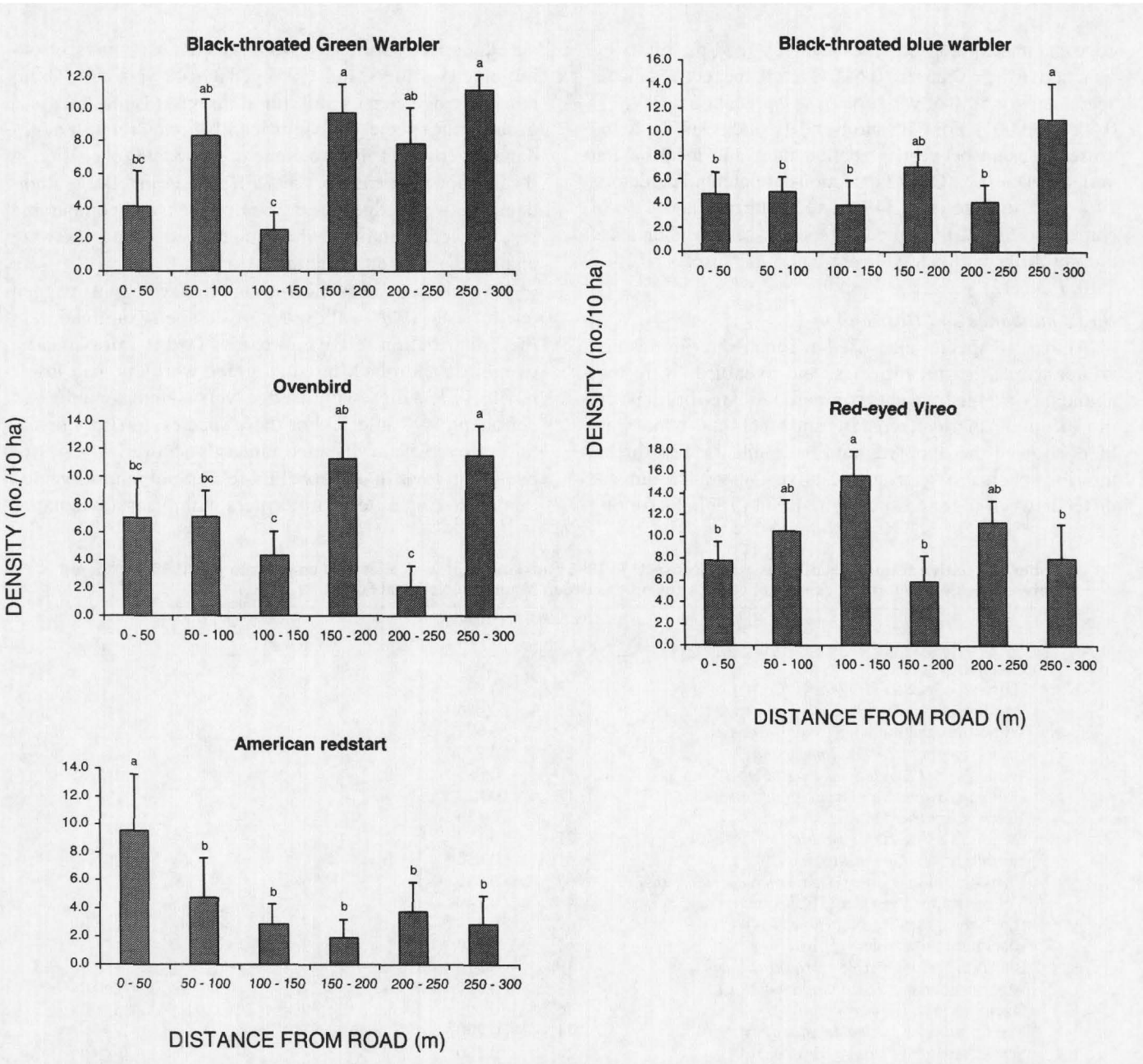

Figure 2. Territory density for 50 m intervals at increasing distance from roads on the Green Mountain National Forest, 1996. For each species, intervals with the same letter did not differ (Duncan Multiple Range test, $df = 30$, $P > 0.1$).

intervals resulted from the tendency of territories to line up in rows parallel to roads. Territories mapped adjacent to roads were restricted to forest habitat rather than extending across the road such that territory centers fell >30 m from the forest-road interface. Densities in the first 50 m interval were relatively low for these species, but did not differ significantly from densities in most other intervals (Figure 2).

In contrast, territory density of American redstarts, also an interior species, was higher within edge versus interior areas (Table 1), and peaked within the 50 m interval closest to roads (Figure 2). Territory density peaked 250–300 m from roads for black-throated blue warblers, and 100–150 m away for red-eyed vireos (Figure 2), and neither species showed differences between edge and interior areas (Table 1).

Discussion

Nest Predation

As indexed by predation levels of artificial nests, nest predators in the study area did not forage differentially with respect to forest-road edges. Predation pressure should be proportional to predator abundance (Andren 1992), and relative abundance of blue jays, red squirrels, and chipmunks, identified as important predators in forested landscapes, did not differ between road-edge and interior transects. Although numerous authors have suggested that blue jays are attracted to forest edges (e.g., Wilcove 1985, Askins 1994, Paton 1994), most studies in our region have not found an association between blue jay abundance and edge habitat (e.g., Lent and Capen 1995, Germaine et al. 1997, King et al. 1998). Research has documented increased activity of mammalian

nest predators within forest habitat adjacent to fields and wide powerline corridors but low activity within these openings, suggesting that such openings may function as habitat barriers (Bider 1968, Chasko and Gates 1982). We frequently observed red squirrels and chipmunks crossing roads in our study area, indicating that such roads may be too narrow to function as barriers for mammalian predators. King et al. (1998) found relative abundance of red squirrels and eastern chipmunks to be marginally correlated with proximity to clearcut edges, proposing that sciurids use resources in both clearcut and forest such that they concentrate at borders between the two habitats. This mechanism should not operate at forest-road edges because roads are unlikely to provide abundant resources for sciurids.

Our finding of no edge effect on nest predation is consistent with most other studies conducted in heavily forested landscapes (reviews in Donovan et al. 1997 and Hartley and Hunter 1998, but see Flaspohler et al. 2001). In contrast, the majority of nest predation studies have been conducted in landscapes highly fragmented by agriculture and development (Donovan et al. 1997) where generalist species such as striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) penetrate forest edges, adding to predation pressure exerted by forest-dwelling predators (Wilcove 1985, Andren 1992). Although these mammalian predators may travel between forest and open habitat along edges of roads (Small and Hunter 1988, Askins 1994), it is plausible that they were not prevalent in our study area due to the limited degree of fragmentation (Donovan et al. 1997, Hartley and Hunter 1998). Similarly, avian nest predators associated with mixed landscapes [e.g., common grackles (*Quiscalus quiscula*) and American crows (*Corvus brachyrhynchos)*] were not detected during point-count surveys. Studies have reported lower rates of predation in increasingly forested landscapes (reviews in Donovan et al. 1997 and Hartley and Hunter 1998), but variation in landscape features within our study area was relatively small (e.g., forest cover: = 93.9 ± 0.39%, range 84.8 to 97.9%) and did not appear to influence predation pressure.

We did find a relationship between predation rates and nest type. Studies comparing predation levels of ground and shrub nests have obtained inconsistent results (e.g., Martin 1992, Hanski et al. 1996), suggesting variability in predator assemblages among study areas (Martin 1987). In our study, predation levels were significantly higher for shrub nests compared to ground nests, possibly reflecting the foraging strategies of the dominant artificial-nest predators (Rudnicky and Hunter 1993). Because blue jays and red squirrels are arboreal and search for prey visually, they may have detected shrub nests more often than ground nests. In contrast, small rodents such as mice, common forest mammals that forage primarily on the ground, have not been identified as important nest predators and may be unable to depredate quail eggs (Hartley and Hunter 1998, DeGraaf et al. 1999).

The final ANOVA model for predation rates included the nest-type effect, but only described 50% of variation in predation rates among transects. The remaining variation likely reflects the patchy distribution of predators, variable in space and time (Leimgruber et al. 1994, Hanski et al. 1996). We found no evidence that predation patterns were influenced by local habitat characteristics including nest concealment. Numerous studies conducted in forested habitat have tested relationships between nest predation and local habitat features, yielding inconsistent results (review in Martin 1992, Hanski et al. 1996).

Bird Abundance and Distribution

Our analyses of relative abundance and territory density of forest birds suggest that narrow roads can influence bird distribution. Four of 18 forest-interior species had lower relative abundance or territory density adjacent to roads, while two forest-interior species showed the opposite pattern. Four of six species categorized as edge nesters had higher relative abundance on edge transects. Considering the ecology of these species and findings from other studies, we believe our results indicate the influence of edge effects rather than factors unrelated to the presence of a forest-road interface.

As found in studies of forest edges associated with wider openings (e.g., Wenny et al. 1993, Lent and Capen 1995, Germaine et al. 1997), numbers of ovenbirds, winter wrens, black-throated green warblers, and hermit thrushes were reduced at road edges relative to interior forest. It has been suggested that passive displacement of territory centers may cause lower detections of territorial males adjacent to forest borders (Kroodsma 1984, Rich et al. 1994, King et al. 1997), providing one explanation for this finding. Indeed, in our study, mapped territories of ovenbirds and black-throated green warblers did not extend into the road, and territory centers were offset from the forest-road interface, tending to line up in rows. Other studies have reported that forest–nonforest interfaces function as territory boundaries for some bird species (Chasko and Gates 1982, Kroodsma 1984, King et al. 1997). However, according to simulations of ovenbird territory distribution, passive displacement does not adequately account for observed reductions in ovenbird density within edge areas, 0–150 m from roads (Ortega and Capen 1999). It is unclear how passive displacement relates to reduced relative abundance of hermit thrushes and winter wrens on edge transects because spot mapping delineated few of their territories.

Differential densities of forest-interior birds relative to road edges may indicate gradients in resource levels. Altered microclimate regimes at forest edges result from increased light levels and heightened exposure to wind and precipitation (Matlack 1993). Invertebrates in leaf litter, a main food source for ground-gleaning ovenbirds, winter wrens, and hermit thrushes, may be sensitive to edge conditions that include increased temperature and diminished litter moisture (Villard et al. 1993). Haskell (2000) found that abundance of soil-dwelling macroinvertebrates was reduced up to 100 m from unpaved roads. Previous research has shown that insectivorous birds respond to gradients in arthropod abundance (Robinson and Holmes 1982) and that territory size is inversely related to prey density (review in Smith and Shugart 1987). We found that territory size of ovenbirds on our study plots was inversely related to distance from roads (Ortega and

Capen 1999), suggesting that a gradient in density of litter invertebrates may be affecting densities of ground-gleaning bird species.

Conditions at road edges may have the opposite effect on the prey of American redstarts. This forest-interior species had higher relative abundance on edge transects and higher territory density within edge areas; similar associations have been reported for other types of forest edges (Collins et al. 1982, Kroodsma 1984, King et al. 1997). In contrast to other forest-interior warblers, redstarts forage mid-canopy, pursuing active prey primarily through "tumble" and "hover" maneuvers (Robinson and Holmes 1982). Blake and Hoppes (1986) documented concentrations of both flying insects and redstarts within tree-fall gaps of deciduous forests, attributing the pattern to increased light and temperature levels in such habitats. Microclimate conditions at forest-road edges may have comparable effects on redstarts and their prey. Forest borders also provide perches adjacent to open habitat, increasing foraging opportunities for fly-catching birds such as redstarts (Blake and Hoppes 1986). In our study, redstart territories were concentrated within the 50 m interval closest to roads, and redstarts were frequently observed foraging at the forest-road border.

Like redstarts, black-and-white warblers are classified in the forest-interior group yet had higher relative abundance at road edges. As bark gleaners, they also have a unique foraging strategy among the forest-interior species common to our study sites. Other researchers have reported positive associations between black-and-white warblers and forest edges (Strelke and Dickson 1980, Collins et al. 1982, Kroodsma 1984), but we are unaware of studies that report on relevant resource levels in these habitats.

Forest-interior species did not appear to actively avoid forest-road interfaces. Consistent with Rich et al.'s (1994) results, relative abundance of forest-interior species as a group was not different on transects adjacent to unpaved roads compared to those 300 m from roads. In addition, spot mapping showed that forest-interior species established territories tangent to the forest-road border. Because northern New England was historically forested with infrequent disturbances to the forest canopy, it is unlikely that forest birds in the region have been exposed to selective pressure to avoid edges (Van Horn et al. 1995, King et al. 1997). Species in the forest-interior category are defined to nest away from edges, but this definition is not based on quantitative analyses (see Whitcomb et al. 1981, Freemark and Collins 1992), and edge avoidance has not been substantiated (Rich et al. 1994, King et al. 1997).

Most edge species had higher relative abundance on edge transects, according to statistical tests for individual species and for the group. Unlike forest-interior species, those classified in the edge category generally have well established associations with forest–nonforest borders (e.g., DeGraaf and Rudis 1986, Lent and Capen 1995). Although habitat measurements revealed no differences in forest structure between edge and interior transects, vegetation plots on edge transects were restricted to the forest canopy. Roadside vegetation consisted of variable strips of grass, herbaceous vegetation, and/or woody vegetation, and likely influenced the presence of edge species. For example, chestnut-sided warblers are low-canopy foragers requiring brushy thickets, but American robins and dark-eyed juncos forage on the ground within low vegetation and directly on the surfaces of unpaved roads (DeGraaf and Rudis 1986, personal observation).

Overall, analyses of bird distribution suggest species-specific responses to fine-scale differences in habitat parameters related to the forest-road interface. For some forest-interior species, these forest borders represented habitat boundaries, thereby affecting the placement of territories. Moreover, differential resource levels relative to roads may have influenced densities of forest birds. Because arthropod groups are influenced by microclimate conditions in differing ways and bird species vary in their diet composition, bird species should exhibit varied responses to edge conditions. Microhabitat differences at forest-road edges may also influence foraging or nesting opportunities for some species. The literature-based categorization of bird species into groups by edge use provided a framework for exploring distributions relative to forest-road edges. However, species-specific results were more instructive for evaluation of mechanisms underlying road-edge effects.

Management Implications

Given the ubiquitous distribution of roads on the Green Mountain National Forest and managed forests in general, habitat quality relative to forest-road edges is relevant to the viability of forest bird populations. At least 20% of the forest area on the northern Green Mountain National Forest is within 150 m of a road, and only 60% of the forested area is >150 m from a forest border, suggesting that edge conditions could influence a significant proportion of a species' regional population.

From the perspective of population viability and management, habitat quality for forest birds should be evaluated by considering both density and reproductive success (Van Horne 1983). We found that relative abundance or territory density of four forest-interior species was higher within interior forest, >150 m from unpaved roads, and no indication that nest predation rates, indexed using artificial nests, differed between edge and interior areas. Although additional measures of reproductive success at forest-road edges should be examined, our results imply that for ovenbirds, winter wrens, hermit thrushes, and black-throated green warblers, habitat quality may be higher >150 m from roads in our study area. Based on measures of territory distribution and nest predation, habitat quality may be higher at forest-road edges for American redstarts, black-and-white warblers, and edge species as a group.

Paton (1994) noted inconsistency among avian studies in the classification of edges and suggested a silviculture-derived definition based on the width of the opening and the height of the adjacent trees. However, it is apparent that such a definition is incomplete. Criteria for defining edges must be framed within the context of specific ecological processes: although levels of predation on artificial nests were not influenced by forest-road borders in our study, distribution

and abundance of forest bird species were affected in varying ways. Furthermore, landscape as well as local factors must be considered when assessing ecological function relative to forest–nonforest borders (Donovan et al. 1997). For example, characteristics of an opening might affect nest predation levels in the adjacent forest by influencing activity patterns of mammalian predators, or they may affect the distribution of forest birds by influencing the occurrence of passive displacement. Landscape context affects predator communities such that forest-road borders may have elevated predation rates in regions more fragmented than our own (Donovan et al. 1997, Hartley and Hunter 1998). Similarly, landscape factors may affect the distribution and abundance of forest-interior birds near edges by influencing predation rates or levels of competition with edge species (Ambuel and Temple 1983, Wenny et al. 1993).

Criteria for identifying functional edges should be based on habitat quality. Because habitat quality is measured by both density and reproductive success, species-specific parameters which themselves interact (e.g., Andren 1992, Wenny et al. 1993), the result is a complex assessment requiring consideration of multiple processes operating over a range of scales. Before such assessments can be accomplished, we must attain a mechanistic understanding of the patterns recorded in numerous edge-related studies of forest birds.

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