

EFFECTS OF FOREST ROADS ON HABITAT QUALITY FOR OVENBIRDS IN A FORESTED LANDSCAPE

YVETTE K. ORTEGA¹ AND DAVID E. CAPEN

Wildlife and Fisheries Biology Program, University of Vermont, Burlington, Vermont 05405, USA

ABSTRACT.—Numerous studies have reported lower densities of breeding Ovenbirds (*Seiurus aurocapillus*) adjacent to forest edges. However, none of these studies has considered habitat use and reproductive success to address mechanisms underlying the observed pattern, and most were conducted in fragmented landscapes and ignored juxtapositions of forest with narrow openings such as roads. We studied the influence of forest roads on Ovenbird density in an extensively forested region of Vermont, evaluating habitat use and reproductive success relative to mechanisms proposed to explain the density-edge relationship. Territory densities on seven study plots were 40% lower within edge areas (0 to 150 m from unpaved roads) than within interior areas (150 to 300 m from roads). We simulated the distribution of Ovenbird territories and concluded that passive displacement, where birds perceive habitat interfaces as boundaries and limit their territories entirely to forest habitat, did not account for the observed density-edge pattern. Territory size was inversely related to distance from roads, providing an alternative explanation for reduced densities near edges and suggesting that habitat quality was higher away from roads. Pairing success was lower within edge areas than within interior zones, but the difference was not statistically significant. The proportion of males that produced fledglings did not differ between edge and interior areas. We conclude that habitat quality for Ovenbirds may be lower within 150 m of unpaved roads in extensive forested landscapes, affecting territory density and possibly reproductive success. Received 28 May 1998, accepted 29 January 1999.

FRAGMENTATION OF CONTIGUOUS FOREST is viewed as a primary factor in recent declines of many populations of songbirds (Whitcomb et al. 1981, Hutto 1988, Terborgh 1989). Studies of area-sensitive species whose densities decline as forest patch-size declines have implicated adverse effects of forest edges on these species (Askins et al. 1990, Paton 1994). Studies of the Ovenbird (*Seiurus aurocapillus*), an area-sensitive Neotropical migrant, document population declines (Askins et al. 1990, Hussell et al. 1992) and sensitivity to edges. Decreased densities of Ovenbirds near edges have been reported in numerous studies (e.g. 1993, Rich et al. 1994, Lent and Capen 1995, Burke and Nol 1998). The Ovenbird has been placed in the "forest-interior" group of species that are thought to nest within the interior of forests and rarely near edges (Whitcomb et al. 1981, Freemark and Collins 1992); yet, it is unclear how the density of edges relate to habitat use and habitat quality.

Lower densities of edge-sensitive species may result from "passive displacement" of territory centers away from forest borders, where birds perceive habitat interfaces as boundaries and limit their territories entirely to forest habitat (Kroodsma 1984, Rich et al. 1994, King et al. 1997). However, reduced densities at edges could also result from lower habitat quality. Differential vegetation structure may limit availability of nesting and foraging sites or cover (Kroodsma 1984, Smith and Shugart 1987). Similarly, Ovenbird prey may be less abundant near edges because of microclimate alterations (Villard et al. 1993, Burke and Nol 1998). In addition, edge-related reductions in pairing success (Van Horn et al. 1995), increased parasitism by cowbirds (Brittingham and Temple 1983), and increased nest predation (King et al. 1996) have been reported for Ovenbirds. Territory size in birds varies inversely with habitat quality (Smith and Shugart 1987), and lower edge densities may result directly from this relationship. Alternatively, inferior habitats may lead to active avoidance of edges (Villard et al. 1993, Wenny et al. 1993, Van Horn et al. 1995), thereby causing lower densities.

¹ Present address: USDA Forest Service, Rocky Mountain Research Station, P.O. Box 8089, Missoula, Montana 59807, USA. E-mail: ortega-yvette/rmrs-missoula@fs.fed.us

Studies reporting edge-related declines in Ovenbird density have not considered relevant patterns in habitat use or reproductive success to address the processes underlying the observed density pattern. Furthermore, most of these studies were conducted in heavily fragmented landscapes, and only one (Rich et al. 1994) examined edges formed by narrow (<25 m) breaks in the forest canopy. In this paper, we examine the influence of forest roads on Ovenbird habitat quality in an extensive forested landscape. After documenting lower densities of territories at forest-road edges, we present data on habitat use and reproductive success to evaluate three possible mechanisms that could produce this pattern: (1) the passive-displacement hypothesis, in which territories located adjacent to roads are limited to forested habitat such that territory centers are displaced from forest-road borders; (2) the territory-size hypothesis, whereby habitat quality is lower within edge areas, resulting in an increase in territory size that limits densities; and (3) the active-avoidance hypothesis, in which habitat quality is lower within edge areas, causing males to avoid edges and locate their territories away from roads.

STUDY AREA AND METHODS

Study area and plot establishment.—Field work was conducted on the northern half of the Middlebury District of the Green Mountain National Forest (GMNF) in Vermont. The region is 94% forested with a scattering of openings that average $3.4 \pm \text{SE of } 0.25$ ha ($n = 1,342$); these openings result from timber harvesting, agriculture, and residential and ski-area development. Roads traverse the forest at a density of 700 m/km², and 70% of them are unpaved.

We established six 9-ha plots and one 7.5-ha plot in northern hardwood forest stands 50 to 150 years in age and dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) and with occasional white ash (*Fraxinus americana*), red maple (*Acer rubrum*), and red spruce (*Pinus rubra*). Plots, selected for their general uniformity of management history and forest composition from a set of 25 randomly selected sites, were located adjacent to dirt and gravel roads of width 7.0 to 10.0 m and at elevations of 550 to 675 m. Each rectangular plot, marked in a 25-m grid, began at the road and extended 300 m into the forest. For consideration of road effects on habitat use and reproductive success, plots were divided into "edge" areas, which were 0 to 150 m from roads, and "interior" areas, which were 150 to 300 m from

roads. We selected 150-m distance classes because they were wide enough to encompass Ovenbird territories and generally were related to the extent of edge effects detected in other studies (e.g. Kroodsmas 1984, Wenny et al. 1993, King et al. 1996). Distance to and size of nearest opening did not differ ($F < 0.77$, $df = 1$ and 12 , $P > 0.40$) between edge areas (distance, $\bar{x} = 417.7 \pm 62.7$ m, range 138.8 to 628.0 m; size, $\bar{x} = 1.6 \pm 1.8$ ha, range 1.8 to 4.8 ha) and interior areas (distance, $\bar{x} = 501.2 \pm 71.4$ m, range 228.8 to 748.4 m; size, $\bar{x} = 1.2 \pm 1.3$ ha, range 0.8 to 3.8 ha).

Distribution of territories.—We delineated territory locations of males using the spot-mapping technique from 31 May through 29 June 1996. We conducted censuses from sunrise to 5 h after sunrise, during which detections of Ovenbirds, including fledglings, were recorded on grid maps. Observers walked systematically (4 ha per h) along the center of each 50-m-wide strip, parallel to the road, pausing at each 50-m grid point for at least 2 min. To increase mapping accuracy and distinguish adults from fledglings, detections of uncertain origin were investigated further. Detections outside of plot boundaries were recorded to improve the mapping of boundary territories (Marchant 1981). We censused plots 10 times each, with visits spaced every two to four days. Territories were defined as clusters of three or more registrations from different spot-mapping visits ($\bar{x} = 13.7 \pm 0.85$ registrations per territory, range 4 to 34, $n = 49$ territories), and adjacent clusters were delineated with mapped countersinging events and simultaneous registrations. Playback tapes of Ovenbird song were used on non-census mornings to aid in the identification of discrete clusters (Falls 1981).

For analyses, we assigned territories to distance classes according to the perpendicular distance between the road and the center of the territory (Van Horn et al. 1995, King et al. 1996), which was defined as the midpoint between the registrations closest and farthest from the road. Densities were calculated as the number of territory centers per 10 ha for each distance class on each census plot.

Pairing success and territory size.—We used a focal-male technique (Gibbs and Faaborg 1990) to assess pairing status and territory size in relation to roads. Individual territorial males on three of our census plots were followed for continuous 90-min periods between sunrise and 1000 EST (12 to 24 June), during which we noted evidence of pairing and mapped singing and foraging locations. Observation sessions were terminated if a bird was silent or unseen for 20 min (Probst and Hayes 1987). Sessions were alternated between edge and interior birds to the extent that logistics allowed. We classified focal males as paired if they were observed interacting with a female within 5 m, carrying nesting material, feeding young, or defending a nest or fledglings (Gibbs and Faaborg 1990, Porneluzi et al. 1993). Focal males with no evidence of pairing after one session were resur-

veyed between 18 June and 3 July following the above protocol but using playback tapes of Ovenbird song to aid in the location of focal males and associated mates or fledglings (Porneluzi et al. 1993). To validate our technique for determining pairing status, we also conducted focal-male sessions on birds known to be paired, using playback tapes in three of five trials.

To determine territory size of focal males, we combined locations from focal-male sessions (in which playback tapes were not used) and spot-mapping censuses. Using a geographic information system (GIS), the central 95% of locations per male were connected to form the minimum convex polygon representing the "total utilized territory" (Zach and Falls 1979, Smith and Shugart 1987). The total number of locations per territory ranged from 16 to 38 and did not differ between edge ($\bar{x} = 26.3 \pm 2.9$, $n = 7$) and interior ($\bar{x} = 25.6 \pm 1.8$, $n = 14$) males ($F = 0.05$, $df = 1$ and 19 , $P > 0.8$). To quantify the degree to which males avoided edge areas on the three focal plots, we used these data to consider the proportion of each distance class occupied by territories. Spot-map locations for three non-focal males were added and connected as described previously for this calculation.

Fledging success.—To complete the mapping of Ovenbird broods, we surveyed each of the seven plots an additional seven times, 2 July through 2 August. Including spot-mapping censuses, plots were visited every two to four days throughout the fledging period (late June to early August). Because fledgling Ovenbirds frequently emit a weak "chip" call and remain with their parents until about 30 days of age, we believe that we detected the majority of broods that fledged (i.e. left the nest) on our plots. During surveys, we walked grids as described for territory mapping, but observers moved at approximately half the rate. All Ovenbird calls and singing males were investigated and recorded on grid maps. For each family group detected, we documented locations and movements of parents and fledglings, as well as physical and behavioral descriptions of fledglings to approximate their ages (Hann 1937).

To index the proportion of territories fledging at least one young within edge and interior areas, brood detections were referenced to territory maps of males. Clusters of brood detections from different visits were considered multiple observations of the same brood unless fledgling ages, time between detections (>21 days), or parental activity (e.g. movements or countersinging events) indicated otherwise. Broods were then assigned to mapped territories based on their proximity and on the movements and countersinging events of associated male Ovenbirds (which continue to exhibit territoriality during the fledgling period [Hann 1937]). We thereby assigned broods to distance classes and excluded broods detected at plot boundaries that were not associated

with mapped territories. We calculated fledging success as the ratio of the number of broods to the number of territories per distance class-study plot. Territories with >25% of their area located outside plot boundaries were excluded from the calculation because of reduced probability of detecting associated broods.

Habitat measurements.—We measured 10 variables considered important in characterizing Ovenbird habitat (Thompson and Capen 1988, Robbins et al. 1989, Van Horn et al. 1995). Three circular 0.04-ha plots were randomly located within the territory of each focal male. As part of a related study (Ortega 1998), plots were also located systematically throughout the study sites, giving habitat data for areas falling outside of Ovenbird territories. At the center of each plot, we measured depth of leaf litter, shrub height, canopy height, and slope. 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 along the transects by counting the number of stems (>1 m tall, <5 cm diameter at breast height [dbh]) within 1 m of the transect. Basal area was estimated using a 2.5 (m²/ha)-factor prism. For trees included in the assessment of basal area, dbh was measured and averaged for each vegetation plot.

Simulations of territory distribution.—We designed a series of simulations to assess whether the passive-displacement hypothesis could describe the observed distribution of Ovenbird territories independent of the territory-size and active-avoidance hypotheses. We used GIS to sequentially place circular, nonoverlapping territories at randomly selected coordinates within areas simulating our study plots. The size of the simulated territories corresponded to the average size of Ovenbird territories on our plots. Following the passive-displacement hypothesis, simulated territories were not permitted to extend into the road. Because the expected distribution of territories within an area is affected by the number of territories placed within it, we conducted a separate simulation for each study plot, holding the number of simulated territories equal to the actual number of mapped territories on the plot. Densities of simulated territories were calculated using the methods described for actual territories. Ten simulations were run for each plot, and the mean density per distance class was used in analyses. To consider the null hypothesis that territories were distributed randomly with respect to roads, simulations were repeated without the passive-displacement constraint.

Statistical analyses.—We used ANOVA to test territory density, territory size, fledging success, and habitat measurements for differences between distance classes of study plots. Simulated densities under the passive-displacement and null models were

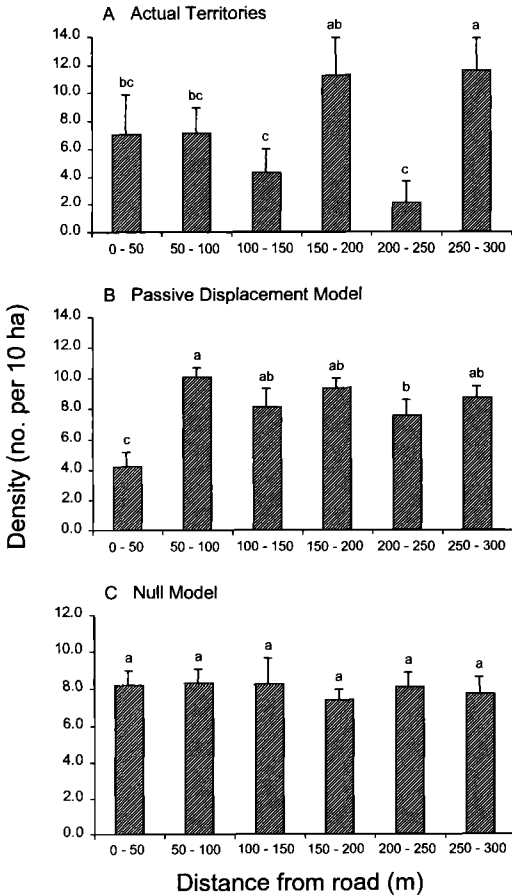


FIG. 1. Comparisons of actual and simulated densities of Ovenbird territories among 50-m intervals at increasing distance from roads. For each density variable, intervals with the same letter do not differ significantly ($P > 0.05$).

compared with densities of actual territories for each distance class separately. Study plot was included in ANOVA models as a blocking factor (Sokal and Rohlf 1981), and multiple comparisons were conducted with Duncan's new multiple range test. We tested assumptions of normality and homogeneity of variance with Shapiro-Wilk and F_{max} tests and applied standard transformation methods where necessary

(Tabachnick and Fidell 1989). Variables that could not be successfully transformed were ranked and then tested with ANOVA.

We used multiple regression analysis to examine territory size as a function of proximity to roads and the ten habitat variables (averaged across vegetation plots per territory). Bivariate (Pearson) correlation coefficients were examined to screen for multicollinearity (Tabachnick and Fidell 1989). Through a backward selection process, variables were eliminated from the regression model until all remaining variables had F -statistics significant at the $P = 0.1$ level. To assess the unique contribution of each variable in a model to the overall variation in territory size, we examined semipartial correlation coefficients (Tabachnick and Fidell 1989). This analysis enabled us to consider the relationship between the size of a territory and its distance from a road when the influence of other habitat variables was statistically removed. We used SAS software for all analyses (SAS Institute 1990).

RESULTS

Patterns of territory distribution.—We delineated 49 Ovenbird territories in the seven plots. Territories tended to occur in rows parallel to roads. Territories comprising the first row did not extend into roads, and their centers were located 30 to 80 m from the forest-road border, giving intermediate densities within 100 m of roads (Fig. 1A). Two distinct peaks in territory density were located 150 to 200 m and 250 to 300 m from roads (Fig. 1A). Territory density was significantly lower within 50 m of roads than that within the interval farthest from roads (Fig. 1A). Overall, densities were 40% lower ($P = 0.01$) within edge areas versus interior areas (Table 1).

Densities of simulated territories did not show patterns of peaks and lows in relation to roads (Figs. 1B, C). For the passive-displacement model, territory density within 50 m of roads was significantly lower than densities in the remaining intervals (Fig. 1B), but densities did not differ between edge and interior areas

TABLE 1. Density (per 10 ha) comparisons for actual and simulated Ovenbird territories within edge (0 to 150 m) and interior (150 to 300 m) areas of study plots. Values are $\bar{x} \pm SE$.

	Edge	Interior	F^a	P
Actual territories	6.2 ± 0.77	9.9 ± 1.02	11.57	0.01
Passive-displacement model	7.5 ± 0.85	8.6 ± 0.73	3.63	0.11
Null model	8.3 ± 0.83	7.7 ± 0.69	2.72	0.15

^a ANOVA, $df = 1$ and 6.

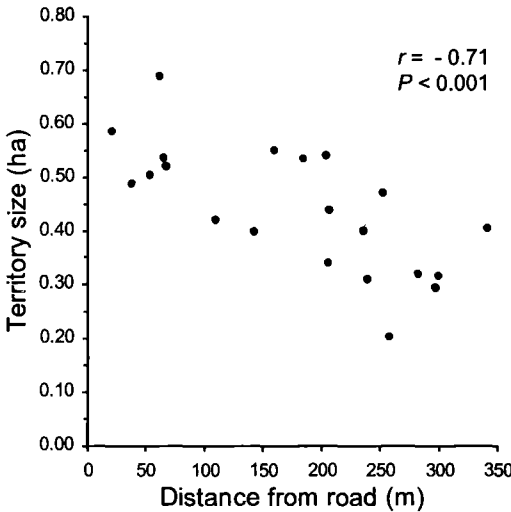


FIG. 2. Relationship between territory size and distance from roads for 21 Ovenbird territories surveyed on the Green Mountain National Forest, 1996.

(Table 1). For the null model, densities did not differ among the intervals (Fig. 1C) or between edge and interior areas (Table 1).

Comparisons of actual and simulated densities revealed significant differences. For the edge class, density of actual territories was lower than densities derived under the passive-displacement and null models ($F = 7.39$, $df = 2$ and 12 , $P < 0.01$; Table 1). For interior areas, the density of Ovenbird territories was higher than densities simulated under the two models ($F = 7.53$, $df = 2$ and 12 , $P < 0.01$; Table 1).

Patterns of habitat use.—Territory size for 21 focal males ranged from 0.20 to 0.69 ha ($\bar{x} =$

0.44 ± 0.029). Edge territories ($\bar{x} = 0.53 \pm 0.032$ ha, $n = 7$) were significantly larger ($F = 7.93$, $df = 1$ and 17 , $P < 0.05$) than interior territories ($\bar{x} = 0.39 \pm 0.028$ ha). Territory size did not differ among study plots ($F = 5.41$, $df = 2$ and 17 , $P > 0.05$), and we pooled across plots for subsequent analyses of territory size. Territory size was negatively correlated with the distance of the territory from the forest-road border ($r = -0.71$, $P < 0.001$; Fig. 2). The proportion of area occupied by territories did not differ between edge ($\bar{x} = 39.6 \pm 2.16\%$) and interior ($\bar{x} = 36.7 \pm 4.28\%$) classes ($F = 0.21$, $df = 1$ and 2 , $P > 0.60$).

Habitat variables measured at random points within Ovenbird territories did not differ significantly between edge and interior areas (Table 2). Ground cover in areas not occupied by territories was significantly higher than at points randomly located within Ovenbird territories, and no additional habitat variables showed significant differences between territory and non-territory points (Table 3).

Regression analysis of territory size resulted in a model with three variables: distance from road, litter depth, and ground cover. This model accounted for 68% of total variation in territory size (Table 4). The independent influence of distance from road accounted for 48% of the variation in territory size ($P < 0.001$), whereas litter depth contributed 17% ($P < 0.01$) and ground cover 8% ($P < 0.05$). Distance from road was not significantly correlated with any other habitat variables ($r < 0.40$), and none of the habitat variables was highly correlated with any other variable ($r < 0.50$). The independent

TABLE 2. Comparison of habitat variables ($\bar{x} \pm SE$) measured at random points within edge (0 to 150 m) and interior (150 to 300 m) Ovenbird territories.

Variable	Edge	Interior	F ^a	P
Basal area (m ² /ha)	28.0 ± 1.30	31.4 ± 1.35	2.64	0.11
Relative basal area of conifers (m ² /ha) ^b	42.2 ± 2.05	39.3 ± 0.83	2.06	0.16
Tree diameter (cm) ^c	1.5 ± 0.01	1.5 ± 0.01	0.01	0.94
Canopy height (m) ^d	4.4 ± 0.13	4.4 ± 0.08	0.00	0.95
Canopy cover (%)	34.3 ± 0.64	33.9 ± 0.47	0.31	0.58
Stem density (stems/ha) ^c	3.6 ± 0.04	3.5 ± 0.04	3.33	0.07
Shrub height (m) ^b	40.9 ± 3.97	40.2 ± 3.45	0.02	0.88
Ground cover (%) ^d	4.2 ± 0.13	4.4 ± 0.16	1.34	0.25
Litter depth (cm)	3.3 ± 0.29	3.1 ± 0.18	0.41	0.53
Slope (%)	17.0 ± 1.52	16.0 ± 1.00	0.45	0.51

^a ANOVA, $df = 1$ and 76 .

^b Rank-transformed values.

^c Log-transformed values.

^d Square-root transformed values.

TABLE 3. Comparison of habitat variables ($\bar{x} \pm SE$) measured at random points within Ovenbird territories and at points not occupied by Ovenbird territories.

	Territory	Non-territory	F ^a	P
Basal area (m ² /ha)	30.0 ± 0.97	30.5 ± 1.56	0.01	0.92
Relative basal area of conifers (m ² /ha) ^b	52.6 ± 1.26	50.0 ± 0.00	1.17	0.28
Tree diameter (cm) ^c	1.5 ± 0.01	1.5 ± 0.02	0.29	0.59
Canopy height (m) ^d	4.4 ± 0.07	4.5 ± 0.16	0.11	0.74
Canopy cover (%)	34.1 ± 0.38	33.4 ± 0.94	0.66	0.42
Stem density (stems/ha) ^c	3.5 ± 0.03	3.5 ± 0.06	0.08	0.78
Shrub height (m) ^b	50.2 ± 3.32	58.2 ± 6.27	1.18	0.28
Ground cover (%) ^d	4.3 ± 0.11	4.8 ± 0.14	7.81	0.01
Litter depth (cm)	3.2 ± 0.16	3.3 ± 0.26	0.07	0.80
Slope (%)	16.4 ± 0.86	17.2 ± 1.68	0.15	0.70

^a ANOVA, df = 1 and 99.

^b Rank-transformed values.

^c Log-transformed values.

^d Square-root transformed values.

influence of distance from road on territory size was significant irrespective of the combination of habitat variables included in the model.

Reproductive success in relation to roads.—Eighty-five percent of focal males were classified as paired, and all of five validation trials yielded confirmation of paired status. The proportion of paired males did not differ among study plots (Fisher exact test, $P > 0.50$); therefore, we pooled data across plots. Pairing success was 79% for edge males ($n = 14$) compared with 92% for interior males ($n = 12$), but the difference was not significant (Fisher exact test, $P > 0.50$), and the power of the test was low (<0.25 at $\alpha = 0.05$; Cohen 1988).

Twenty-two of 44 territories fledged at least one young; 19 of these broods were clearly associated with reference territories. Each of the remaining three brood detections straddled boundaries of multiple territories located within the same 150-m distance class, so selection of a single reference territory was not pertinent. Fledging success did not differ between edge ($\bar{x} = 42.9 \pm 8.86\%$) and interior areas ($\bar{x} = 50.1 \pm 8.95\%$; $F = 0.43$, $df = 1$ and 6 , $P = 0.54$).

DISCUSSION

The density of Ovenbird territories was lower within edge areas than within interior areas. The absence of territory centers within 30 m of roads, the relatively low territory density in the first 50-m interval from a road, and observations of focal males with territories adjacent to roads indicated that territory centers were passively displaced away from roads. Other researchers have reported that forest birds locate territory boundaries at human-made edges (Chasko and Gates 1982, Kroodsmma 1984, Rich et al. 1994, King et al. 1997).

However, passive displacement alone does not adequately explain the 40% reduction in density within edge areas versus interior zones. The density of actual territories within edge areas was lower than that simulated under passive-displacement and null models that held territory size constant. Under the passive-displacement model, the simulated density for edge areas was not different from the interior density because fine-scale displacement of territory centers within the first 50-m interval did

TABLE 4. Regression model of Ovenbird territory size with distance from road and habitat variables. Model $F = 12.25$, $R^2 = 0.68$, $P = 0.002$.

Variable	b	SE	t	P
Intercept	0.2620	0.1111	2.36	0.03
Distance from road	-0.0008	0.0002	-5.08	0.0001
Litter depth	0.0698	0.0230	3.03	0.008
Ground cover	0.0056	0.0026	2.13	0.05

not significantly depress densities within the 150-m edge zone.

Variation in territory size with distance from roads provides a more plausible explanation for lower territory density within edge areas. Based on the distribution of actual territories (Fig. 1A), it is evident that a moderate number of territories occurred within 150 m of roads, whereas two peaks in density were evident within the interior distance class. Territories adjacent to roads, with diameters averaging 25% larger than territories farthest from roads, were distributed over a relatively wide area compared with territories that formed density peaks within interior areas, giving a lower density of territories within edge areas. Still, territories abutted roads and occupied approximately equal proportions of edge and interior areas, suggesting that Ovenbirds did not actively avoid forest-road borders.

Territory size and habitat quality.—Numerous studies of territory size in Ovenbirds and other species have documented an inverse relationship between prey density and territory size (see Smith and Shugart 1987). Invertebrates in leaf litter, the main food source of Ovenbirds (Hann 1937), may be less abundant within forest edges because of altered microclimates (e.g. decreased litter moisture and increased litter temperature; Matlack 1993, Villard et al. 1993, Burke and Nol 1998). Litter fauna adjacent to unpaved roads could also be sensitive to accumulation of dust particles and heavy metals (Lagerwerff and Specht 1970, Forman and Godron 1986).

Vegetation structure may serve as a "structural cue" to prey density, thereby regulating habitat selection and territory size (Smith and Shugart 1987). Ovenbirds in our study selected areas with low ground cover, and territory size decreased as ground cover decreased. However, regression analysis indicated that proximity to roads was more important than other habitat variables in describing territory size. Vegetation structure within territories did not differ between the two distance classes, and when effects of other habitat variables were removed, distance of territories from roads explained 48% of the variation in territory size, further suggesting an effect on habitat quality that was independent of vegetation structure.

Various hypotheses provide mechanisms for edge effects on territory size, based on the pre-

mise of differential prey density. As with vertical vegetation structure, Ovenbirds may use proximity to edges as an index to prey density, adjusting territory size accordingly (Villard et al. 1993). Alternatively, Ovenbirds may use "direct monitoring" of resource levels to regulate territory size (see Smith and Shugart 1987). Territories may also be smaller away from roads because of increased levels of intraspecific competition for habitat with higher food quality (Smith and Shugart 1987).

Reproductive success and habitat quality.—We have suggested that the observed reduction in the density of Ovenbird territories near roads, driven by an increase in territory size, is indicative of lower habitat quality within edge areas. However, habitat quality should also be evaluated in terms of reproductive success (Van Horne 1983, Vickery et al. 1992). We observed high rates of pairing, which is typical for Ovenbirds in forest-dominated landscapes (Villard et al. 1993, King et al. 1996, Sabine et al. 1996). Although the difference was not statistically significant, pairing success was lower within 150 m of roads than in interior areas. Female Ovenbirds may select territory holders by directly assessing resource levels or by using territory density (Villard et al. 1993) or territory size (Verner 1964) as an index. Alternatively, female Ovenbirds may select mates directly, preferring older males that are likely to concentrate in higher-quality habitats (Sherry and Holmes 1989, Holmes et al. 1992). Both of these mechanisms predict that pairing success is higher for males holding interior territories, if resource levels are indeed lower at edges.

Reduced food supply should lead to lower productivity (Rodenhouse and Holmes 1992), but we found no differences in fledging success between edge and interior areas. Other studies of Ovenbirds in extensive forests report levels of fledging success comparable to ours (Porneluzi et al. 1993, King et al. 1996). However, local-scale variation in prey availability may cause more subtle differences in clutch size, nesting success, and frequency of multiple brooding that are not reflected in measures of fledging success (Martin 1992).

Landscape effects.—Patterns in habitat use and reproductive success relative to edges should also be evaluated in terms of landscape context. Contrary to our findings, Wenny et al. (1993) reported that in forest fragments of central

Missouri, Ovenbird territories occupied lower proportions of edge areas within 100 m of fragment borders compared with interior areas more than 200 m from borders. Working in the same region, Van Horn et al. (1995) documented a significant relationship between Ovenbird pairing success and proximity to edges. Researchers have suggested that these edge-related patterns reflect avoidance of areas with increased levels of nest predation and brood parasitism (Van Horn et al. 1995). Such a behavior could have evolved in the historically fragmented region studied by Wenny et al. (1993) and Van Horn et al. (1995), where forest edges were prevalent in presettlement times and may have had increased levels of predation and parasitism (Van Horn et al. 1995). Because northern New England was historically forested (Hornbeck and Leak 1991), Ovenbirds in our region may not have been exposed to selective pressure to avoid edges. Edge-related reduction in density and pairing success recorded in highly fragmented landscapes could also be the direct result of decreased survivorship and productivity at edges, given that numerous studies have documented edge-related increases in nest predation and parasitism within a landscape context (e.g. Wenny et al. 1993, Van Horn et al. 1995). However, most studies conducted in extensively forested landscapes have not reported diminished nest survival at edges (e.g. Hanski et al. 1996, Donovan et al. 1997). Predation rates on artificial nests placed in forested habitat adjacent to roads in our study area did not differ from those placed 300 m from roads (Ortega 1998), and Brown-headed Cowbirds (*Molothrus ater*) were relatively uncommon on the GMNF (Ellison 1990a, Coker and Capen 1995). Thus, it is unlikely that edge-related effects on territory size and density in our study were related to predation or parasitism. Instead, as described above, local-scale differences in food availability at edges could cause effects on density and productivity that are independent of landscape context. Although edge effects on food supply may be more pronounced in landscapes with lower connectivity of forest patches and sharper microclimate gradients (Sabine et al. 1996, Burke and Nol 1998), our results provide indirect evidence that gradients in prey availability exist within extensively forested landscapes.

Management implications.—Habitat quality for

Ovenbirds may be lower within 150 m of unpaved roads in extensive forest landscapes, affecting territory density and possibly reproductive success. Thus, ubiquitous distribution of roads through forested areas potentially represents a significant cumulative reduction in abundance of the species (Rich et al. 1994). If edge effects extend 150 m from roads and other human-made openings, 40% of the forested area in the northern half of the GMNF may represent lower-quality habitat for Ovenbirds. Roads themselves account for more than 50% of the edge area in the region.

Given the overall abundance of Ovenbirds in the region (Ellison 1990b) and the observed level of fledging success, there is no indication that viability of the local population is threatened. However, diminished productivity would limit the forest's capacity to function as a population source for forest fragments outside the GMNF that are population sinks (Pulliam 1988). As private lands become increasingly susceptible to subdivision and development, public lands such as the Green Mountain National Forest will become more important sources of contiguous forest habitat needed to sustain populations of forest-interior species (Askins 1994). Our study suggests that even narrow forest roads should be viewed as sources of habitat fragmentation that exert negative effects on the quality of habitat for forest-interior species such as the Ovenbird.

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LITERATURE CITED

- ASKINS, R. A. 1994. Open corridors in a heavily forested landscape: Impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* 22: 339–347.
- ASKINS, R.A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7:1–57.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.

- BURKE, D. M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- CHASKO, G. C., AND J. E. GATES. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* No. 82.
- COHEN, J. 1988. *Statistical power analysis for the behavioral sciences*, 2nd ed. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- COKER, D. R., AND D. E. CAPEN. 1995. Landscape-level habitat use by Brown-headed Cowbirds in Vermont. *Journal of Wildlife Management* 59: 631–637.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON III. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. *Ecology* 78:2064–2075.
- ELLISON, W. G. 1990a. The Brown-headed Cowbird (*Molothrus ater*). Pages 368–369 in *The atlas of the breeding birds of Vermont* (S. B. Laughlin and D. P. Kibbe, Eds.). University Press of New England, Hanover, New Hampshire.
- ELLISON, W. G. 1990b. The Ovenbird (*Seiurus aurocapillus*). Pages 314–315 in *The atlas of the breeding birds of Vermont* (S. B. Laughlin and D. P. Kibbe, Eds.). University Press of New England, Hanover, New Hampshire.
- FALLS, J. B. 1981. Mapping territories with playback: An accurate census method for songbirds. Pages 86–92 in *Estimating numbers of terrestrial birds* (C. J. Ralph and J. M. Scott, Eds.). *Studies in Avian Biology* No. 6.
- FORMAN, R. T. T., AND M. GODRON. 1986. *Landscape ecology*. John Wiley and Sons, New York.
- FREEMARK, K., AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443–454 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- GIBBS, J. P., AND J. FAABORG. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. *Conservation Biology* 4:193–196.
- HANN, H. W. 1937. Life history of the Oven-bird in southern Michigan. *Wilson Bulletin* 49:145–237.
- HANSKI, I. K., T. J. FENSKE, AND G. J. NIEMI. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *Auk* 113:578–585.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETIT. 1992. Multiple breeding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321–333.
- HORNBECK, J. W., AND W. B. LEAK. 1991. Ecology and management of northern hardwood forests in New England. U.S. Forest Service General Technical Report NE-159.
- HUSSELL, D. J. T., M. H. MATHER, AND P. H. SINCLAIR. 1992. Trends in numbers of tropical- and temperate-wintering migrant landbirds in migration at Long Point, Ontario, 1961–1988. Pages 101–114 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- HUTTO, R. L. 1988. Is tropical deforestation responsible for the reported decline in Neotropical migrant populations? *American Birds* 42:375–379.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727–736.
- KING, D. I., C. R. GRIFFIN, AND R. M. DEGRAAF. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. *Conservation Biology* 10:1380–1386.
- KING, D. I., C. R. GRIFFIN, AND R. M. DEGRAAF. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bulletin* 109:239–245.
- KROODSMA, R. L. 1984. Effect of edge on breeding forest bird species. *Wilson Bulletin* 96:426–436.
- LAGERWERFF, J. V., AND A. W. SPECHT. 1970. Contamination of roadside soil and vegetation with cadmium, nickel, lead, and zinc. *Environmental Science and Technology* 4:583–586.
- 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.
- MARCHANT, J. H. 1981. Residual edge effects with the mapping bird census method. Pages 488–491 in *Estimating numbers of terrestrial birds* (C. J. Ralph and J. M. Scott, Eds.). *Studies in Avian Biology* No. 6.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 101–114 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- MATLACK, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185–194.
- ORTEGA, Y. K. 1998. Roads as edges: Effects on habitat use and reproductive success of forest birds. M.S. thesis, University of Vermont, Burlington.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17–26.
- PORNELUZI, P., J. C. BEDNARZ, L. J. GOODRICH, N. ZAWADA, AND J. HOOVER. 1993. Reproductive performance of territorial Ovenbirds occupying

- forest fragments and a contiguous forest in Pennsylvania. *Conservation Biology* 7:618–622.
- PROBST, J. R., AND J. P. HAYES. 1987. Pairing success of Kirtland's Warbler in marginal vs. suitable habitat. *Auk* 104:234–241.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- RICH, A. C., D. S. DOBKIN, AND L. J. NILES. 1994. Defining forest fragmentation by corridor width: The influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* 8:1109–1121.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat requirements of breeding forest birds of the mid-Atlantic states. *Wildlife Monographs* No. 103.
- RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357–372.
- SAS INSTITUTE. 1990. SAS/STAT user's guide, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SABINE, D. L., A. H. BOER, AND W. B. BALLARD. 1996. Impacts of habitat fragmentation on pairing success of male Ovenbirds, *Seiurus aurocapillus*, in southern New Brunswick. *Canadian Field-Naturalist* 110:688–693.
- SHERRY, T. W., AND R. T. HOLMES. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): A removal experiment. *Behavioral Ecology and Sociobiology* 25:327–333.
- SMITH, T. M., AND H. H. SHUGART. 1987. Territory size variation in the Ovenbird: The role of habitat structure. *Ecology* 68:695–704.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, San Francisco.
- TABACHNICK, B. G., AND L. S. FIDELL. 1989. Using multivariate statistics. Harper Collins, New York.
- TERBORGH, J. 1989. *Where have all the birds gone?* Princeton University Press, Princeton, New Jersey.
- THOMPSON, F. R. III, AND D. E. CAPEN. 1988. Avian assemblages in seral stages of a Vermont forest. *Journal of Wildlife Management* 52:771–777.
- VAN HORN, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112:98–106.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. *Evolution* 18:252–261.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Is density an indicator of breeding success? *Auk* 109:706–710.
- VILLARD, M.-A., P. R. MARTIN, AND C. G. DRUMMOND. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768.
- WENNY, D. G., R. L. CLAWSON, J. FAABORG, AND S. L. SHERIFF. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. *Condor* 95:968–979.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on the avifauna of the eastern deciduous forest. Pages 125–205 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharp, Eds.). Springer-Verlag, New York.
- ZACH, R., AND J. B. FALLS. 1979. Foraging and territoriality of male Ovenbirds (Aves: Parulidae) in a heterogeneous habitat. *Journal of Animal Ecology* 48:33–52.

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