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INFLUENCE OF FOOD ABUNDANCE, NEST-SITE HABITAT, AND FOREST FRAGMENTATION ON BREEDING OVENBIRDS

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ABSTRACT.—Between 1994 and 1996, we determined the density and pairing success of territorial male Ovenbirds (*Seiurus aurocapillus*) in 31 forest fragments in southern Ontario. The density and pairing success of territorial males increased significantly with area of the woodlot core. We tested the hypotheses that area-related changes in food abundance and the availability of suitable nest sites are the causal mechanisms limiting female settlement in small forest fragments. Our results indicated that Ovenbirds chose territories with significantly higher prey biomass than occurred at randomly selected sites in the woodlot. Within Ovenbird territories, prey biomass was 10 to 36 times higher in large woodlots than in small woodlots. Invertebrate biomass at randomly located quadrats in large woodlots was more than twice that found at random sites within small woodlots, and was slightly greater than prey biomass within Ovenbird territories in small fragments. Leaf litter was deeper within Ovenbird territories in large woodlots than at random sites in both large and small forests, and within Ovenbird territories in small woodlots. Ovenbirds in large woodlots selected nest sites that were more than 250 m from the forest edge, distances that were not obtainable in small forest fragments. The lack of potential nest sites, combined with lower food abundance in small fragments, may explain why female Ovenbirds find small fragments unsuitable as breeding sites, and hence why so few males secure mates in small fragments. Understanding the cause of deterioration of breeding sites with decreasing woodlot area should underscore efforts to preserve larger tracts of forest to provide adequate nesting habitat for forest-interior migrants. *Received 25 November 1996, accepted 12 June 1997.*

THE OVENBIRD (*Seiurus aurocapillus*) is a ground-nesting passerine that typically breeds in the interior of large tracts of forest in northern and northeastern North America (Van Horn and Donovan 1994) and obtains most of its prey from the forest floor. As a species apparently linked to the forest interior, and requiring 100 to 885 ha of contiguous forest for breeding (Robbins 1979, Robbins et al. 1989), Ovenbirds have been the focus of numerous studies examining the adverse effects of forest fragmentation on Neotropical migrants (Wander 1985, Gibbs 1988, Gentry 1989, Wenny 1989, Van Horn 1990, Porneluzi et al. 1993, Villard et al. 1993, Donovan 1994, Robinson et al. 1995). Forest fragmentation may negatively affect reproductive success of Ovenbirds by reducing rates of pairing success (up to 75 %; Wander 1985, Gibbs and Faaborg 1990, Villard et al. 1993) or increasing rates of nest predation (Wilcove 1985, Robinson et al. 1995) and parasitism by Brown-headed Cowbirds (*Molothrus ater*; Brittingham and Temple 1983, Robinson et al. 1995).

Sex ratios are thought to be biased in favor of males, either because of high rates of predation of females on the nest (Gibbs and Faaborg 1990) or low overwinter survival due to poor competitive abilities with males at wintering sites (Rappole and Warner 1980). Thus, competition for females could be expected to be intense. Certain characteristics important to female Ovenbirds during nest-site selection may be less abundant or absent on small tracts of forest. Although habitat preferences vary in different parts of their range (Collins 1983), Ovenbirds consistently choose territories in mature forests (tree height 16 to 22 m) with high (60 to 90%) canopy cover (Smith 1981, Sweeney and Dijak 1985, Robbins et al. 1989). Relative to random sites, nesting Ovenbirds select areas with lower ground cover, larger trees (Smith and Shugart 1987), and flatter areas (Wenny 1989). Female Ovenbirds also select nest sites where the leaf litter is thick and at distances greater than 20 m from the forest edge (Hann 1937, Van Horn and Donovan 1994).

Lower levels of reproductive success in small forest tracts may result from inadequate foraging and nesting sites (Wenny 1989). Small

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fragments may not reach the internal humidity levels necessary to sustain invertebrate food supplies in the leaf litter (Southwood 1966, Wenny 1989). Small fragments with elevated levels of light and desiccation of leaf litter (Lee 1987) are likely to have reduced densities of litter fauna, which in turn may support lower densities of Ovenbirds (Gibbs 1988). If birds cue on features of the habitat that are correlated with prey abundance, rather than assessing food resources directly (Smith and Shugart 1987), then large forests may be preferred to small fragments if fragment size is correlated with food abundance.

We examined the density and pairing success of territorial male Ovenbirds as a function of woodlot size, core area, and local forest cover within 31 forest fragments. We hypothesized that woodlot size affects preferences of female Ovenbirds, and hence pairing success, through its influence on the availability of suitable nest sites and food resources. We measured microhabitat characteristics at Ovenbird nest sites and at random sites to ascertain if these varied as a function of woodlot size. Finally, we measured the biomass of arthropods in the leaf litter at random sites in the forest and within Ovenbird territories to determine whether food abundance differed relative to woodlot size.

STUDY AREA AND METHODS

Study sites.—This study was conducted in Peterborough County in the Great Lakes-St. Lawrence Lowlands of southern Ontario, Canada (Hills 1959). The region was surrounded by drumlins, beveled surfaces, and plains with glacial moraine deposits. Elevations range from 75 to 408 m with an average of 305 m (Wickware and Rubec 1989).

Sixty-nine different woodlots within the Peterborough district were selected for point-count censuses based on the amount of core area, defined as forest at least 100 m from the edge (Gates and Gysel 1978, Ranney et al. 1981, Temple 1986, Wenny 1989). Woodlots ranging in size from 0.06 to 351 ha in core area (12 to 2,353 ha total woodlot area) were chosen from upland deciduous forests with reference to a series of forest cover maps prepared from LANDSAT imagery taken in 1984 and 1985 and a geographic information system database (Hounsell et al. 1992). Woodlot fragments were surrounded primarily by cultivated fields. Patches subjected to severe recent disturbance from lumbering, grazing, or fire were excluded, but landowners within some of the study sites removed small amounts of lumber for firewood.

The vegetation at all study sites was dominated by mature sugar maple (*Acer saccharum*), with smaller amounts of American beech (*Fagus grandifolia*), ironwood (*Ostrya virginiana*), and white ash (*Fraxinus americana*). Less abundant canopy species included eastern hemlock (*Tsuga canadensis*), white elm (*Ulmus americana*), white pine (*Pinus strobus*), and eastern white cedar (*Thuja occidentalis*). Regardless of fragment size, all stands had a closed canopy (>70%) and similar levels of plant diversity and habitat heterogeneity within the 100-m^2 vegetation plots centered on the point-count locations (Burke unpubl. data).

Abundance estimates.—The presence and abundance of Ovenbirds were determined on all 69 forest fragments using a modified version of the Forest Bird Monitoring Program protocol developed by Welsh (1995). Ten-minute point counts conducted from 25 May to 5 July 1994 and 26 May to 23 June 1995 were used to record the locations of all birds seen or heard within 100 m. Because of the large number of sites, each was surveyed once between 0430 and 0830 EST. All point counts were conducted in similar habitats within the core areas. No surveys were conducted when rain, fog, or high winds could interfere with detection. We took the average number of individuals between 1994 and 1995 and used these data as an unbiased estimate of the effects of area on Ovenbird abundance.

Density and pairing success.—Thirty-one woodlots (0.06 to 351 ha core area) known to contain Ovenbirds were selected from the original 69 woodlots used for point counts. Due to the inherent bias in this method, we used these density estimates only to support results obtained from point counts. Only one of this subset of woodlots was associated with housing, with a single house located at the edge of the forest >300 m from our study site. Different study plots were established for eight study sites that were used in more than one year (Table 1).

Our research focused on male Ovenbirds that had partial or complete territories within the core area of each of the 31 forests. We mapped out smaller plots (4 to 16 ha) within the core area of all but the smallest tracts to monitor Ovenbird density and pairing success. Each plot was visited from 0.5 h before sunrise to 1030, at least four times between 18 May and 6 July in each year, to ensure that all territorial males were recorded and mapped. Density of territorial males was calculated as the number of territories lying entirely within the plot plus the estimated proportion that each additional territory overlapped the plot (i.e. 0.25, 0.33, 0.5, etc.). Presumably, this is a more accurate estimate of density than that obtained using a value of 0.5 regardless of what percentage each territory actually overlapped the plot (Villard et al. 1993).

To determine pairing success, each focal male was followed for at least 90 min of "track time" or until pairing status was determined with confidence,

TABLE 1. Description of study sites. Total area is a measure of total woodlot area, core area is the amount of forest >100 m from the forest edge, and local forest cover is the amount of forest within a 2-km radius of the study site.

Study site	Year sampled	Total area (ha)	Core area (ah)	Local forest cover (ha)
Burke	1994, 1995, 1996[a]	48.88	0.31	182.56
Trent 1	1994	11.75	0.13	167.38
Trent 2	1995	26.69	0.06	168.88
Greenaway	1995	51.13	0.25	264.00
Dorin	1995	74.88	0.13	225.06
Chapman	1994, 1995	65.81	0.88	288.44
Godfrey	1994, 1995, 1996[a]	37.38	3.00	558.50
Saarimaki	1994	74.89	8.25	216.69
Darling	1995	156.50	8.00	471.56
CarMichael	1994	41.13	8.88	338.06
Smigelow	1994, 1995	73.88	9.75	586.17
Herkimer Point	1994, 1995, 1996[a]	209.50	79.75	432.13
Burnham Woods	1994, 1995[a]	22.25	4.00	293.63
Hay	1994, 1995	50.00	15.00	237.00
Wornoff	1995	109.06	17.38	239.31
Ted Spearing	1994, 1995, 1996[a]	69.63	14.88	342.19
St. John	1994	364.88	15.19	412.88
Whistance-Smith	1995	364.88	13.06	428.94
TRT-medium	1995, 1996	2,352.75	14.81	747.13
Brackenridge	1994, 1995, 1996[a]	79.69	32.25	283.81
Howson	1994	123.56	61.44	376.94
Stewart's Woods	1995	132.36	45.63	429.13
Pickett	1994	510.75	163.00	464.69
Fleetwood Creek	1994, 1995, 1996[a]	748.94	79.69	558.63
TRT	1995, 1996	2,352.75	133.00	593.06
Long Sault	1995, 1996[a]	2,352.75	350.88	618.69
Torchia	1996	2,352.75	99.00	781.44
TRT-small	1995	151.50	5.63	511.50
McColl-Large	1995, 1996	227.25	22.00	402.00
McColl-Small	1995, 1996	227.25	2.40	395.06
Cowey	1995	79.63	24.69	389.69

[a] New area was surveyed within repeated sites.

whichever came first (Gibbs and Faaborg 1990, Villard et al. 1993). If a male was no longer in sight or could not be heard, timing was stopped until the male could be relocated. If the male was not discovered within 5 min, then the session was terminated and restarted at a later date. Territorial males were classified as paired if they were observed interacting with a female, calling to a mate, carrying food or nesting material, or defending or feeding fledglings. During the preincubation period, pairs were readily detected by the female's high *tsip* calls (Lein 1980), which frequently are given during male–female interactions and in response to the mate's song. Males classified as unpaired were visited later in the season to verify their status.

We combined data sets on density and pairing success from all three years of the study and treated each woodlot as an independent observation. Data collected from fragments sampled in more than one year were averaged regardless of whether a different plot was established within the site (for eight woodlots; Table 1). We conducted multiple regression analyses to determine the relative effect of total woodlot area, core area, and amount of local forest cover on the number of territorial males and percent pairing success. We used local forest cover as a measure of the degree of patch isolation based on the amount of forest cover within a 2-km radius of the site (determined from LANDSAT data and a geographic information system).

Food abundance.—Ovenbirds feed primarily by walking slowly and continuously, gathering invertebrates from litter on the surface of the forest floor (Holmes and Robinson 1988, Van Horn and Donovan 1994). In 1995, a preliminary study was done to determine if there were any differences in Ovenbird food abundance among woodlots of varying size. Significant differences were found at nest sites within 17 woodlots, warranting a more detailed evaluation of food abundance in 1996.

In 1995, litter samples were collected in August from 0.25-m^2 quadrats in 17 woodlots ranging in size from 0.25 to 361 ha in core area. All litter was collected within the quadrat, down to the humus layer where decomposition occurred, and litter depth was measured to the nearest 0.1 mm. Within each woodlot, one sample was collected 5 m from each of a maximum of five Ovenbird nest sites (where nests were located) or within male territories (hereafter both are termed "territory sites"). Leaf litter was sifted by hand; invertebrates were placed in 75% ethanol and then air dried and weighed after 24 h.

To save time in processing invertebrates in 1996, litter samples were collected from smaller 0.018-m^2 circular quadrats within nine woodlots ranging in size from 0.13 to 361 ha in core area (22 to 2,353 ha total woodlot area). We collected three or four samples from randomly selected sites within each woodlot (including both core and edge habitats), and one sample from each of three Ovenbird territories, and measured litter depth to the nearest 0.1 mm. One litter sample was collected early (21 May to 16 June), middle (17 June to 17 July), and late in the breeding season (18 to 31 July) at each site, yielding a total of 163 samples. All samples were collected between 1000 and 1300 on days without rain or high winds. Each sample was placed in a Berlese funnel under a 25-watt bulb for 48 h (Stenger 1958). Litter invertebrates were placed in 75% ethanol, counted, and measured. Dry mass was taken from a subsample of invertebrates and extrapolated to give the relative mass of litter invertebrates from each sample at each site.

Because Ovenbirds do not seem to feed selectively (Stenger 1958), we assumed that all of the litter organisms in our samples were potential food items. In 1996, there was no significant difference ($P = 0.43$) in seasonal changes in prey abundance, so all samples were grouped regardless of the day they were collected.

We analyzed the invertebrate data from each year separately due to differences in sampling and sorting techniques. We found a stepwise relationship between woodlot size and area, warranting an ANOVA test. Woodlots <20 ha in core area formed one group ($\bar{x} = 6.76$ ha, range 0.06 to 17.38 ha), and woodlots >20 ha formed a second group ($\bar{x} = 99.21$ ha, range 22 to 351 ha), which we subsequently termed small and large woodlots, respectively. Because variance was proportional to the mean for litter biomass, we log-transformed this variable prior to analysis. We used the split-plot model (PROC GLM; SAS Institute 1985) to remove variation caused by multiple samples within the same woodlots from the total variation. With this design, we specified the error term as woodlot nested within size class to determine the effects of woodlot size and sample (nest site vs. random site) on biomass of litter invertebrates.

Nest-site selection.—Microhabitat was measured from mid-June to mid-August at 32 random and 36 nest sites in 1995 and at 38 random and 35 nest sites in 1996. A 1-m radius circle centered on the Ovenbird nest was used to determine nest-site microhabitat (Petit et al. 1988). At each site the following variables were measured: (1) distance and direction to the nearest edge; (2) litter depth; (3) percent nest concealment; (4) percent cover of litter, bare ground, and vegetation in all layers from the herbaceous layer to the canopy; (5) percent slope; (6) nest position along a slope; (7) distance to nearest tree in the four cardinal compass directions; and (8) basal area of living and dead trees (using a prism sweep). Most of these variables have been deemed as important parameters for describing Ovenbird habitats elsewhere (Sweeney and Dijak 1985, Van Horn 1990, Van Horn and Donovan 1994). Two-way ANOVA was used to examine the effects of sample (random vs. nest), woodlot size (small vs. large), and the interaction between these effects on the various nest-site habitat variables.

We measured litter depth during nest-site evaluation and combined the data with measurements taken when litter samples were collected. Because the data exhibited the same step-function relationship with a break at 20 ha, we analyzed them using the same split-plot design used in the analysis of litter invertebrate mass.

RESULTS

Density estimates.—Ovenbirds were virtually ubiquitous in our study area, occurring in 66 of the 69 woodlots surveyed. Point-count data revealed a significant increase in the number of singing males with increasing woodlot core area ($F = 5.99$, df = 1 and 67, $P = 0.017$). Woodlot area and local forest cover did not contribute significantly to the multiple regression ($P > 0.15$ and $P = 0.11$, respectively). Based on spot mapping, Ovenbird densities ranged from 0.33 males per 10 ha on the smaller woodlots to 8.3 males per 10 ha on the largest fragment, and increased significantly with increasing woodlot core area ($r^2 = 0.638$, $F = 51.04$, df = 1 and 29, $P < 0.0001$). The abundance indices obtained from point counts were significantly (albeit weakly) correlated with the density of territorial males calculated from spot mapping ($r = 0.36$, $P = 0.048$).

Pairing succes.—Ovenbird pairing success increased most significantly with increases in woodlot core area ($r^2 = 0.684$, $F = 62.86$, df = 1 and 29, $P < 0.0001$; Fig. 1). Pairing success ranged from 0% on the smallest fragments to 100% on the largest fragments. Pairing success was not significantly correlated with point-count density indices ($r = 0.30$, $P = 0.11$) but was highly correlated with densities of terri-

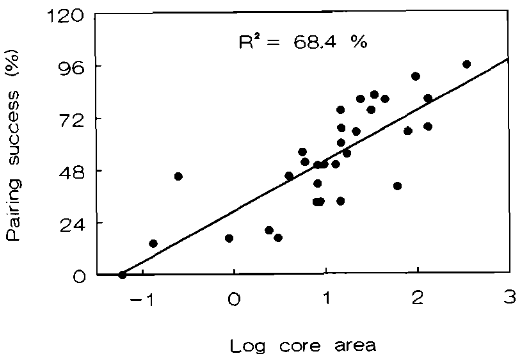

FIG. 1. Relationship between woodlot core area and pairing success of territorial male Ovenbirds. Data were collected from 1994 to 1996 in Ovenbird territories from 31 different woodlots ranging from 0.06 to 351 ha in core area.

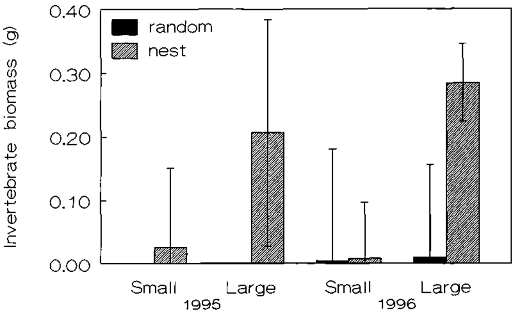

FIG. 2. Biomass of litter invertebrates ($\bar{x}$ ± SE) within Ovenbird territories and at random sites in small (<20 ha core area) and large (≥20 ha) woodlots. Data are presented for nest sites only in 1995 because no samples were collected from randomly located sites within the 17 woodlots ($n = 51$). In 1996, 163 litter samples were collected from 9 woodlots.

torial males obtained from spot mapping ($r = 0.74$, $P < 0.0001$).

Food abundance.—Biomass of litter invertebrate was significantly higher within Ovenbird territories than at randomly located sites (1996, $F = 5.84$, df = 1 and 9, $P = 0.046$) and significantly higher in large compared with small fragments (1995, $F = 10.52$, df = 1 and 15, $P = 0.005$; 1996, $F = 5.59$, df = 1 and 7, $P = 0.05$; Fig. 2). In large fragments (>20 ha in core area), invertebrate biomass within Ovenbird territories was 10 to 36 times higher than in forests <20 ha. Average invertebrate biomass was higher at random sites in large woodlots than at nest sites in small woodlots.

Nest-site evaluation.—In general, Ovenbird nest sites were located on mid- to upper slopes and were characterized by low percent cover of bare ground (<7%), moderate herbaceous and sapling cover, low seedling and shrub cover, high canopy cover, deep litter layer, moderate slope, and distances of about 3 m from the nearest tree (Table 2). Of these characteristics, distance to edge, litter depth, percent cover of bare ground, and percent cover within the seedling

TABLE 2. Microhabitat characteristics ($\bar{x}$ ± SE) at Ovenbird nest sites and randomly selected sites. Variables were measured at 70 random sites and 71 nest sites within 31 forest fragments to determine the effects of sample (random vs. nest) and woodlot size using two-way ANOVA.

	Small fragments		Large fragments					
Characteristic	Nest	Random	Nest	Random	F^a	P	F^b	P
Dist. from edge (m)	125.51 (18.48)	81.92 (8.93)	250.78 (29.20)	192.14 (31.38)	7.24	0.008	22.32	0.0001
Bare ground (%)	11.12 (2.88)	18.00 (4.06)	4.83 (2.46)	5.91 (1.70)	2.64	0.101	8.75	0.0037
Litter (%)	57.07 (6.16)	61.88 (5.66)	82.26 (3.41)	77.45 (4.46)	0.38	0.540	15.94	0.0001
Herbaceous (%)	45.81 (5.91)	25.82 (4.81)	25.78 (3.23)	25.44 (4.38)	3.43	0.066	4.80	0.030[c]
Seedling (<0.5 m; %)	12.28 (3.13)	7.37 (1.82)	28.13 (3.56)	25.62 (4.03)	3.51	0.060	27.29	0.0001
Shrub (0.5 to 2 m; %)	13.04 (3.14)	11.91 (2.51)	26.45 (4.87)	32.41 (5.76)	0.00	0.963	14.61	0.0002
Sapling (2 to 10 m; %)	24.60 (5.69)	27.62 (4.90)	27.34 (5.19)	46.48 (6.24)	3.20	0.076	3.77	0.055
Canopy (%)	78.00 (3.92)	67.01 (5.07)	72.63 (5.19)	69.14 (5.20)	1.82	0.180	0.09	0.760
Slope (%)	9.31 (1.32)	11.36 (1.66)	10.64 (1.46)	10.67 (1.30)	0.34	0.563	0.02	0.880
Nearest tree (m)	3.31 (0.50)	4.04 (1.14)	3.16 (0.20)	2.50 (0.19)	0.04	0.851	1.60	0.208
Basal area (m^2/ha)	26.05 (1.89)	27.10 (1.51)	26.95 (2.05)	24.41 (1.80)	0.14	0.707	0.24	0.626

[a] Random vs. nest-site effect.

[b] Size effect.

[c] Significant interaction.

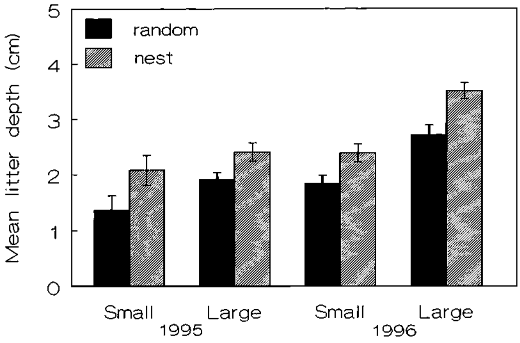

FIG. 3. Litter depth ($\bar{x}$ ± SE) within Ovenbird territories and at random sites within small (<20 ha) and large (≥20 ha) forest fragments. In 1995, 94 litter-depth measurements were taken from 22 woodlots; in 1996, 216 measurements were taken from 11 woodlots.

layer were chosen in proportions that differed from availability (Table 2).

Small forest tracts contained a significantly lower percentage of litter, a higher percentage of bare ground, and a significantly reduced seedling layer and shrub layer (Table 2). More important, random sites within small tracts contained little core area, and hence had few sites available for nesting at distances of 190 m from the edge, i.e. distances that Ovenbirds appear to prefer ($\bar{x}$ = 190.3 ± SD of 20.7 m). Small tracts at randomly selected sites also lacked deep litter, which is important in nest-site selection by Ovenbirds (Fig. 3).

DISCUSSION

We identified some of the factors that may contribute to differential densities and pairing success (and hence productivity) of Ovenbirds on large versus small forest fragments. Small woodlots seemed to be poor habitats for Ovenbirds in terms of food supply, with both random and nest sites containing a low abundance of litter invertebrates. Large forests contained sites rich in food supply. However, because biomass of litter invertebrates at randomly selected sites was much lower than at nest sites, Ovenbirds appeared to have preferentially selected territories rich in food within large forest tracts. In small tracts, Ovenbirds were unable to choose optimal habitats, and all sites may have been poor with respect to prey biomass. Therefore, the higher pairing success of males in large forests may have resulted from an area-dependent change in food supply (Ambuel and Temple 1983).

In our study area, habitat features (habitat heterogeneity, plant species richness, canopy cover) of woodlots within 0.04-ha circles were similar (Burke unpubl. data). However, certain microhabitat variables at nests, including distance to nearest edge and depth of leaf litter, differed significantly with changes in woodlot core area. Therefore, low pairing success may have been caused by females selecting habitats based on leaf-litter depth, a feature that might be assessed directly or that might be correlated with prey biomass. Villard et al. (1993) suggested that female Ovenbirds avoid breeding in areas that border open habitats. Because Ovenbirds avoided edges (see also Kroodsma 1984) and preferred a deep litter layer (see also Van Horn 1990), females may have preferred males with territories on large versus small fragments, explaining the low pairing success of males in small fragments. Females may be more likely to select territories based on features that enhance reproduction (nest-site availability and food abundance), whereas males may be more likely to select territories based on features that enhance territory defense or mate attraction (e.g. song perch availability; Sedgwick and Knopf 1992).

Edge effects may contribute to the apparent area effects (Gentry 1989), and because they are correlated with area, edge-related factors may be causal mechanisms for area-sensitivity (Van Horn 1990). Desiccation of leaf litter is most pronounced near the forest edge and could contribute to edge avoidance by nesting Ovenbirds (Wenny 1989). Ovenbirds forage almost exclusively on arthropods in the leaf litter (Hann 1937, Stenger and Falls 1959), which are particularly susceptible to desiccation (Southwood 1966) that accompanies forest fragmentation (Lovejoy et al. 1986). Sites with increased relative humidity and moisture at the forest floor, as well as increased litter depth, provide a more favorable environment for litter arthropods, and these factors are more typical of large rather than small fragments (Saunders et al. 1991). Female Ovenbirds may respond to horizontal characteristics such as distance to the nearest forest edge, which may influence prey abundance through its effect on litter moisture (Villard et al. 1993). They also may use habitat cues to assess habitat quality, such as vegetational cues that reflect prey abundance (Smith and Shugart 1987).

Forest edge appears to have a negative influence on Ovenbird reproductive success (Wander 1985, Gentry 1989, Van Horn 1990). In Missouri, Ovenbird densities were lower within the first 100 m from the edge (Wenny et al. 1993), and significantly fewer males with territories adjacent to forest edges were mated (Gentry 1989, Van Horn 1990). Van Horn (1990) showed that the response of Ovenbirds to forest edge extended 300 m into the forest, and distance to edge seemed to be the most important source of variance in pairing success (although litter depth and tree height also were important). We found that Ovenbirds avoided nesting near habitat edges, which may have been due to increased predation and parasitism by Brown-headed Cowbirds (*Molothrus ater*) at nonforest edges (Gates and Gysel 1978, Wilcove 1985, Freemark et al. 1995).

As expected, larger tracts of forest contained higher densities of Ovenbirds, and more territorial males were paired in large tracts than in small tracts. Based on preliminary results, there also was an indication that nesting success increased with increasing woodlot core area (Burke and Nol unpubl. data). However, pairing success was not correlated with densities based on point counts. These results may provide forest management guidelines contrary to those based on censusing techniques, because in many chiefly monogamous species, such as the Ovenbird, song output (and hence detectability) declines severely once a bird is paired (Best 1981, Gibbs 1988). Censuses conducted after pairing has occurred may lead to the incorrect conclusion that less-suitable habitats are preferred, because they are populated by a larger proportion of singing (i.e. unmated) males than are the truly preferred habitats (Van Horne 1983, Gibbs 1988).

Our results are similar to those from other regions where the landscape is heavily fragmented by agriculture and urbanization, including New Jersey (Wander 1985), Missouri (Gibbs and Faaborg 1990, Van Horn 1990, Donovan et al. 1995) and eastern Canada (Villard et al. 1993). The influence of local forest cover on Ovenbird density and pairing success was minimal. Our patch-isolation measure contributed little to the relationship between pairing success and landscape features, which highlights the importance of preserving single large tracts of forest regardless of landscape connectivity. Compared with Ovenbirds in forest-dominated landscapes, birds inhabiting fragmented landscapes are much more likely to suffer from reductions in pairing success and food supply. Recent evidence from forest-dominated landscapes in New Brunswick revealed that Ovenbirds within mature forest fragments surrounded by plantations or regenerating stands tend to exhibit low isolation and high connectivity and are not subjected to the same adverse effects to their food supply (Sabine et al. 1996). It is less likely that edge effects, desiccation of leaf litter, or sharp gradients in microclimate and microhabitat would occur in forest-dominated landscapes to the degree that is typical of woodlot fragments surrounded by agriculture. The higher connectivity of this landscape would benefit organisms that have reduced dispersal capabilities, in particular litter-inhabiting arthropods, compared with highly fragmented landscapes where organisms need to disperse 100s or 1,000s of meters to the next nearest patch. These results suggest that the negative effects of fragmentation might occur at a much larger fragment size in landscapes dominated by agriculture than in those dominated by forests (Sabine et al. 1996).

Although it has been suggested that forest patches smaller than 5 ha in core area represent intrinsically poor habitats for Ovenbirds (Wander 1985), our results seem to indicate that the highest-quality habitats (i.e. those with higher prey abundance and higher availability of suitable nest sites) are not obtained in fragments smaller than 20 ha in core area, or at least 80 ha in total woodlot size. From a management perspective, we recommend that a single large tract of forest with a core area greater than 20 ha is better for Ovenbirds than are several small tracts (see also Freemark and Collins 1992). Tracts of forest with the lowest perimeter-to-area ratio also will provide the largest amount of core interior habitat (Ranney et al. 1981, Temple 1986). Although Ovenbirds are common throughout their range, further fragmentation or loss of habitat could lead to the collapse of regional populations of some forest birds, including Ovenbirds (Donovan et al. 1995). Habitat improvements may not be an adequate substitute for the presence of large tracts of forest.

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