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POPULATION DENSITY, HABITAT SELECTION AND MINIMUM AREA REQUIREMENTS OF THREE FOREST-INTERIOR WARBLERS IN CENTRAL MISSOURI[1]

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Abstract. Ovenbirds (*Seiurus aurocapillus*), Kentucky Warblers (*Oporornis formosus*), and Worm-eating Warblers (*Helmitheros vermivorus*) were censused in central Missouri to determine breeding population densities in three forest tracts large enough to satisfy minimum area requirements estimated in an earlier study. Densities of Kentucky Warblers and Ovenbirds were significantly higher in a large forest tract (>800 ha) than in two 300 ha forests. Worm-eating Warblers bred only in the large forest. Kentucky Warblers and Ovenbirds had larger territories in the two sites with lower population density. The three sites had similar vegetation structure but significantly different topography and edge/area ratios. Habitat selection, analyzed with principal component analysis and log-linear models, was significantly different among the three species and different among the three sites. Edge/interior ratio and topographic features contribute to differences in population densities observed among the three sites. Area requirements may be larger than those estimated by the incidence function.

Key Words: Population density; habitat selection; area requirements; Oporornis formosus; Seiurus aurocapillus; Helmitheros vermivorous; *habitat fragmentation.*

INTRODUCTION

Many populations of migratory passerines that breed in the forests of eastern North America and winter in the neotropics are declining (e.g., Robbins et al. 1989b, Finch 1991). Although the available data concerning continent-wide population declines are not conclusive (Askins et al. 1989), local populations in the eastern United States clearly are reduced by forest fragmentation (Robbins 1979, Whitcomb et al. 1981, Lynch and Whigham 1984, Hayden et al. 1985, Askins et al. 1987, Lynch 1987). Small, insectivorous, ground-nesting birds (e.g., many Parulinae) are among the most adversely affected by forest fragmentation; they are typically absent from small forest fragments throughout their range (Ambuel and Temple 1983, Blake and Karr 1984, Robbins et al. 1989a). Several causes for these local extinctions and declines in fragmented regions have been suggested, including increased nest predation (Gates and Gysel 1978, Wilcove 1985), competition from edge or non-forest species (Ambuel and Temple 1982), and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Brittingham and Temple 1983).

Species that are frequently absent from small forest fragments are referred to as "area-sensitive" (Robbins 1979). Conservation of area-sensitive species should be based, in part, on the area of suitable habitat necessary to support a local population. A major problem with this approach, however, has been that definitions of area requirements have not been consistent. Beer et al. (1956) used the term to refer to the smallest area in which a territory could be established. Similarly, Galli et al. (1976), Forman et al. (1976), and Blake (1983) described the smallest forest fragment in which a particular species occurred as its minimum area requirement.

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More recently, the need for area requirements to reflect the amount of habitat necessary to support a viable population led to development of the incidence function (Diamond 1975, 1978), in which frequency of occurrence of each species is plotted against area of habitat. The size class at which 100% (or maximum) occurrence is reached is the recommended minimum area requirement. This method has been used by Robbins (1979) and Hayden et al. (1985) to estimate area requirements for birds in Maryland and Missouri, respectively. Robbins et al. (1989a) also used the incidence function but suggested that 50% of the maximum occurrence be used as an estimate of the minimum area required. Another method is to extrapolate from population density the area necessary to support a population of a critical size (Soule 1980, Shaffer and Samson 1985, Thiollay 1989).

One problem with basing estimates of minimum area requirements on incidence functions is that the area of maximum occurrence is determined by the presence of at least one territorial individual in each fragment of that particular size. In many cases, however, the presence of an individual may not indicate the presence of conspecifics, let alone a viable population.

A second problem with the incidence function is that some area-sensitive species do not attain 100% occurrence at any size class (e.g., Hayden et al. 1985, Robbins et al. 1989a). In such cases, a forest of the recommended area may not even contain the species in question. In other words, the incidence function alone does not predict suitable habitat and area is only one of many variables that may be important in determining habitat quality.

In this study, we focused on three species sensitive to forest fragmentation throughout the eastern deciduous forests: Ovenbird (*Seiurus aurocapillus*), Kentucky Warbler (*Oporornis formosus*), and Worm-eating Warbler (*Helmitheros vermivorus*). Hayden et al. (1985), using the 100% occurrence criterion, estimated the area requirements for these species in central Missouri to be at least 300 ha. Our study sites were among those studied by Hayden et al. (1985). The purposes of this study were to compare population densities of the three focal species at isolated sites meeting the estimated minimum area requirements to those in a large continuous forest, and to compare habitat selection in the isolated and continuous sites. These data could show to what extent forest tracts meeting the minimum area requirements actually supported populations, and whether or not habitat characteristics affected avian population variation.

STUDY SITES

Censuses were conducted in two isolated forests of at least 300 ha in Callaway County, Missouri, near Millersburg and Fulton, and a larger forest of over 800 ha near Ashland in Boone County. Before European settlement of this region the three sites were contiguous (Giessmen et al. 1986). The large forest ("Ashland") is included in the T.S. Baskett Wildlife Research and Education Center (38°44′N;92°12′30″W) and is connected to forest along the Missouri River. The Fulton site (38°54′N;91°57′30″W) is a privately owned 340 ha forest surrounded by cropland. Our census area at Fulton was located in the eastern half of the tract. The Millersburg site (38°53′N; 92°04′30″W) is a 300 ha section of the Cedar Creek Unit of the Mark Twain National Forest. Logging had opened approximately 25% of the canopy seven years before our censuses, leaving densely vegetated clearcuts scattered around the site. The entire site is surrounded by cropland and pasture. Both Millersburg and Fulton are over 1 km from the nearest 100 ha forest tract, and for both sites less than 20% of the land within a 5 km radius was forested. In contrast, forest covered nearly 80% of land within 5 km of Ashland (Gibbs 1988). The vegetation of all sites is mostly mature secondary forest dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.).

METHODS

Population density. Approximately 160 ha of each site were censused by spot-mapping (Robbins 1970) during mid-May–June of 1985–1988. The area censused at each site was divided into three census units of about 50 ha. Each unit was visited five times in 1985, six times in 1986 and 1987, and 10 times in 1988 from sunrise until approximately five hours after sunrise. At the end of each field season all observations for each species at each census unit were transferred to a single acetate overlay. Territories were defined as clusters (Robbins 1970) of at least two (in 1985–1987) or three (in 1988) occurrences of territorial males from different visits. Average population densities over the four-year study period for Ovenbirds and Kentucky Warblers at Ashland were compared with each of the isolated sites separately with Student's t-tests for samples with unequal variances (Sokal and Rohlf 1981). The significance level for multiple comparisons was adjusted according to the Bonferroni technique (Holm 1979).

Total population sizes of territorial males were estimated by multiplying the density by the total area of the site. The number of breeding pairs was based on Gibbs and Faaborg (1990) as follows: 67% of Kentucky Warbler males had mates at all three sites; only 25% of Ovenbird males were paired at the two smaller forests, while 75% were paired at the large forest. Approximately 80% of Worm-eating Warblers were mated at the large forest. Thus, the total populations are less than twice the number of territorial males.

Vegetation. We sampled vegetation on 0.04 ha circular plots, generally following the methods described by James and Shugart (1970). Within each plot we measured 31 variables, including: canopy closure, percent ground cover, ground cover height, percent litter cover, litter depth, number of woody stems taller than 1 m and less than 2.5 cm diameter at breast height (dbh), all living and dead trees greater than 2.5 cm dbh (recorded in one of 10 size classes), percent ground cover in grasses, forbs and woody vegetation, and maximum canopy height.

Vegetation plots were located at five randomly selected sites within known territories and at randomly selected sites outside boundaries of known territories. We sampled 27 Ovenbird territories (135 plots), 26 Kentucky Warbler territories (127 plots [two territories had four and three sample plots, respectively]), 11 Worm-eating Warbler territories (55 plots), and 131 random plots. The number of plots measured at each site was approximately equal except for Worm-eating Warblers which had only one measurement in the isolated sites. For the analysis, the mean habitat values were calculated for each territory while the habitat values for random plots were used as recorded in the field.

Circular plot vegetation data were analyzed with principal component analysis (PCA) from the SAS statistical package (SAS Institute Inc. 1985). The first two components, which maximized the amount of variation in two-dimensional space, were used in constructing graphs. Because of the large number of variables measured, we used cluster analysis (Jolliff 1972, 1973) to select a smaller set for inclusion into PCA. A representative variable was selected from each cluster of correlated variables. Seven clusters were identified, and we selected the variable to which a forest manager could best relate. These were: (1) number of small woody stems, (2) canopy coverage, (3) basal area of live trees (calculated from tree size class data), (4) basal area of dead trees (as above), (5) ground cover height, (6) percent ground cover, and (7) litter depth.

Only the random plots were used to determine the component loadings (eigenvectors) for PCA. We used the loadings for the first two components from the random plot information in an analysis of the bird data: the mean vegetation characteristics for each bird's territory were weighted using these loading factors and plotted with the random plot information to determine if the bird information fit within the random plot data. Another PCA was conducted for Ovenbirds and Kentucky Warblers separately to determine if they selected vegetation characteristics similarly among the three study forests.

Topography and edge. In addition to vegetative parameters, we analyzed topographic features of the study sites that may be selected by the focal species. A transparency with a 0.25 ha grid was placed over photocopies of topographic maps (enlarged 200%) of each site. Four variables, with mutually exclusive states, that were considered potentially important for habitat selection are: (1) topographic location (upland and ridge top, upper slope, intermediate slope, lower slope, bottomland); (2) slope (steep, moderate, flat); (3) drainage (primary stream, secondary stream, none) and (4) edge (forest/nonforest edge, stream edge, none). Upper slope locations were adjacent to upland or ridge-top sites and lower slope locations were adjacent to bottomland. An intermediate slope location either spanned the entire slope between upland and bottomland or was located between upper slope and lower slope. We defined a steep slope as more than two 6.1 m contour intervals within one 0.25 ha block, a moderate slope as one or two intervals, and flat as less than one interval within the block.

After the above variables had been described for all three sites, the 0.25 ha grid overlay was placed over the acetate sheets with the birds' territories. This was done without the topographic maps underneath and separately for each species to avoid biasing results. Any block of which at least one-half was included in one or more territories of the particular species in consideration was defined as "selected" by that species. One block was randomly chosen to represent each territory for analysis.

Log-linear models (from SYSTAT 5.0) on five-way contingency tables (four-way for Worm-eating Warbler) were used to examine interactions among variables. To simplify this analysis, variable states mentioned above were collapsed as follows. Topographic locations (designated L in the models) were reduced to upper (upland and upper slope) and lower (bottomland and lower slope) categories. Intermediate locations were assigned to a category based on the most common designation of the other blocks in that particular territory. In territories where no majority existed, intermediate locations were assigned randomly. Drainage (D) and edge (E) each were collapsed to present and absent categories (but stream edges were not included in the edge category in this analysis). The study area (A) was included as a fifth variable for Ovenbird and Kentucky Warbler. Models were fitted with a stepwise selection procedure until the simplest, best fitting model was found (Fienberg 1977). The P-values indicate the probability that the given model fits the observed frequencies.

Edge effect. At Fulton and the largest portion of Millersburg, we calculated relative density of Ovenbirds and Kentucky Warblers as a function of distance from forest edge. Using the 0.25 ha grid overlay, we counted the number of 0.25 ha blocks included in at least one bird's territory in concentric bands 100 m wide (two blocks). Relative density was expressed as average proportion of each 100 m wide band used by each species over the four year period. Relative densities as a function of distance from forest edge approached a normal distribution and were compared with ANOVA and Duncan's New Multiple Range Test (Ott 1988).

RESULTS

Population density. During 1985–1988, average densities of Ovenbird and Kentucky Warbler at the large forest were significantly greater than those at both smaller forests (Table 1). Kentucky Warbler had significantly higher mean density at Ashland than at Fulton (t = 5.7, df = 6, $P <$ 0.005) and Millersburg (t = 3.2, df = 6, $P <$ 0.05). Ovenbirds had a similar trend of higher density at Ashland than at Fulton (t = 4.9, df = 6, $P <$ 0.025) and Millersburg (t = 6.3, df = 6, $P <$ 0.005). Ovenbirds were not found at the northernmost portion of Millersburg and that area was not included in the calculation for density. None of the three species used the whole area of any study site, so we also compared densities in occupied parts of the study areas. These densities in utilized habitat also were higher at Ashland than the two smaller sites for Kentucky Warblers (Fulton: t = 3.85, df = 6, $P <$ 0.005; Millersburg: t = 4.41, df = 6, $P <$ 0.005) and Overbirds (Fulton: t = 3.02, df = 6, $P <$ 0.025; Millersburg: t = 4.9, df = 6, $P <$ 0.005).

TABLE 1. Average population density of breeding birds from 1985–1988, estimated total number of territorial males, and estimated number of breeding pairs of three warblers at one large continuously forested site (Ashland), and two isolated forest fragment sites.

Site	Average density males/10 ha (SD)	Total # males	Breeding pairs
Kentucky Warbler			
Ashland	1.82 (0.31)	145	98
Fulton	0.91 (0.05)	31	20
Millersburg	1.29 (0.11)	38	26
Ovenbird			
Ashland	1.73 (0.28)	138	104
Fulton	0.94 (0.17)	32	8
Millersburg	0.66 (0.20)	20	5
Worm-eating Warbler			
Ashland	2.13 (0.45)	170	136
Fulton	0.00[a]		
Millersburg	0.00[b]		

[a] Present but not breeding (see text).
[b] Never recorded.

Worm-eating Warblers had slightly higher density than the other two species in the large forest but were not recorded regularly at either of the two smaller forests (Table 1). Individual Worm-eating Warblers were recorded at Fulton in all four years, but were so wide-ranging and infrequently observed that no territories could be defined. No more than two singing males were observed in any one year and no nests were found. We never observed this species at Millersburg.

Vegetation. The mean values for the representative vegetation variables included in PCA of the random plots and Ovenbird, Kentucky Warbler and Worm-eating Warbler territories are presented in Table 2. Table 3 shows the eigenvectors for these variables within Principal Components I and II for the random plots, Ovenbirds, Kentucky Warblers and Worm-eating Warblers.

The data from the random plots on the three study sites overlapped extensively (Fig. 1) sug-

TABLE 2. Mean values of the representative vegetation variables included in PCA for random plots, as well as Oven bird, Kentucky Warbler and Worm-eating Warbler territories at the three study forests, 1985–1986.

	Random $n = 131$		Ovenbird $n = 27$		Kentucky Warbler $n = 26$		Worm-eating Warbler $n = 11$	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
No. of small woody stems/m^2	0.30	0.20	0.31	0.12	0.30	0.12	0.42	0.15
Percent canopy coverage	93.11	7.75	96.40	3.18	97.15	3.46	95.80	2.46
Basal area of live trees (m^2/ha)	11.05	3.77	11.23	1.60	10.42	1.55	10.74	1.96
Basal area of dead trees (m^2/ha)	1.12	1.12	0.97	0.39	0.85	0.54	1.06	0.57
Ground cover height (cm)	10.75	6.41	11.14	4.33	15.60	4.05	8.46	2.46
Percent ground cover	37.48	18.03	38.17	12.20	45.91	7.64	35.27	6.69
Litter depth (cm)	2.11	0.82	2.07	0.63	1.66	0.63	1.97	0.42

gesting that the sites are structurally similar for the first two components. Pooled data for Ovenbirds, Kentucky Warblers and Worm-eating Warblers on all sites showed that all three species selected territories with vegetation characteristics from within the range of the random plots (Fig. 2). This result indicates that our sampling scheme adequately characterized the study sites.

Comparisons of vegetation characteristics selected by birds could be made only for Kentucky Warblers and Ovenbirds because Worm-eating Warblers were found only at the large forest. Both the Ovenbird (Fig. 3) and Kentucky Warbler (Fig. 4) data showed considerable overlap among study areas, indicating that the birds were selecting similar sites on all forests. Although the pooled data for all three forests (Fig. 2) showed overlap between Kentucky Warblers and Ovenbirds, an analysis of the large area alone shows virtually no overlap. At this forest, mean values for per-

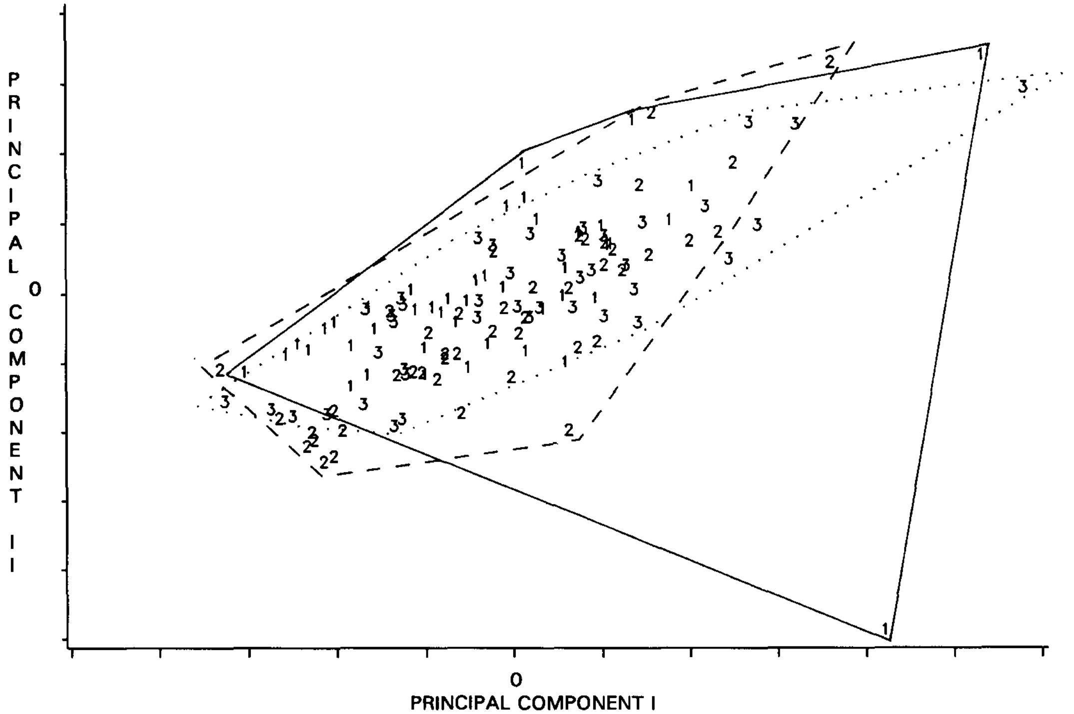


FIGURE 1. Principal component analysis of the random vegetation plots showing the similarity of the Ashland (1), Millersburg (2), and Fulton (3) forests.

TABLE 3. Results of PCA of vegetative parameters at random plots, and within territories of Ovenbirds, Kentucky Warblers and Worm-eating Warblers at the three study forests, 1985–1986.

	Random		Ovenbird		Kentucky Warbler		Worm-eating Warbler	
	Principal component		Principal component		Principal component		Principal component	
	I	II	I	II	I	II	I	II
Total variance accounted for (%)	31.9	19.5	38.8	23.4	37.7	29.0	35.0	25.8
Eigenvectors								
Number of woody stems	0.35	0.59	0.38	−0.00	−0.33	0.41	−0.24	0.50
Percent canopy coverage	−0.25	0.38	−0.50	0.23	0.46	−0.26	0.13	−0.39
Basal area of live trees	−0.20	0.21	0.21	−0.48	−0.28	0.15	−0.40	0.08
Basal area of dead trees	−0.20	0.06	−0.03	−0.28	0.21	0.56	0.30	0.07
Ground cover height	0.61	0.01	0.29	0.61	0.45	0.40	0.52	0.39
Percent ground cover	0.60	−0.10	0.48	0.41	0.30	0.45	0.60	0.20
Litter depth	−0.00	0.67	0.50	−0.32	−0.51	0.25	−0.22	0.63

cent ground cover and ground cover height were significantly higher ($P < 0.01$) in Kentucky Warbler territories than in Ovenbird territories. The mean number of woody stems also was higher in Kentucky Warbler plots than Ovenbird plots, but the difference was not quite significant ($0.05 < P < 0.01$). No differences were found at the other two study areas.

Topography and edge. In contrast to vegetative parameters, topographic features showed consid-

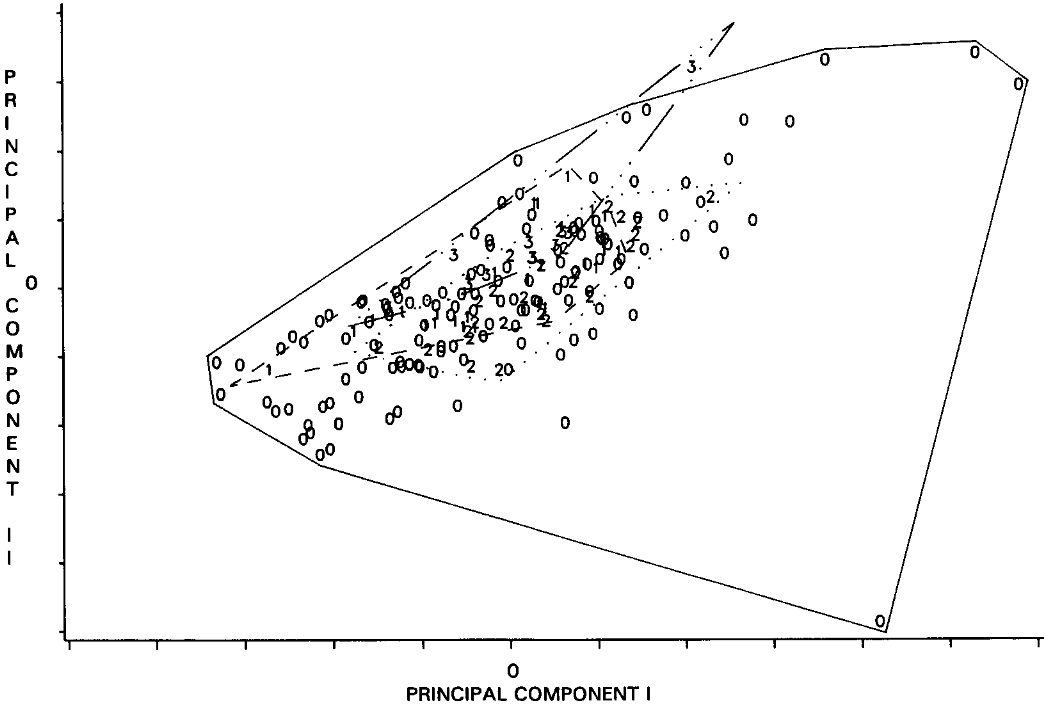


FIGURE 2. Principal component analysis showing vegetative features of Ovenbird (1), Kentucky Warbler (2), and Worm-eating Warbler (3) territories as subsets of the available habitat sample in random sites (0) at all three study sites.

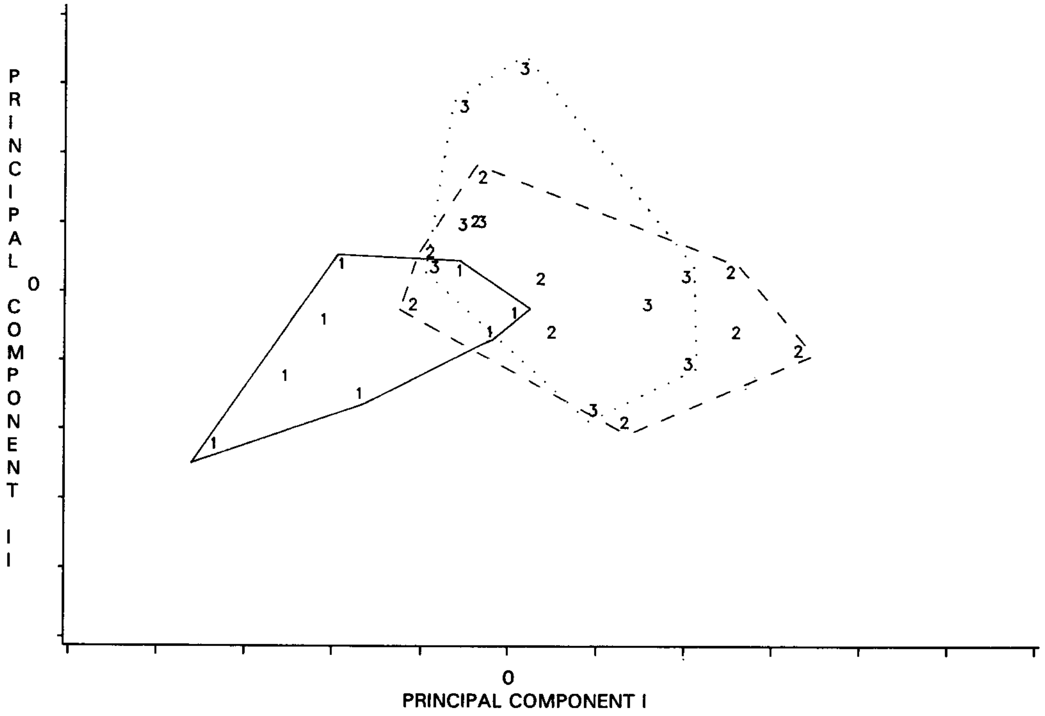


FIGURE 3. Principal component analysis of vegetative features of Ovenbird territories at Ashland (1), Millersburg (2), and Fulton (3).

erable differences among the forests (Fig. 5). The difference in topography was mainly a result of very little upland or upper slope and a predominance of intermediate slope at Millersburg compared to the other forests ($\chi^2 = 157$, df = 8, $P < 0.001$). Much of the ridgetop forest at Millersburg had been cut (and thus not counted), leaving most of the mature forest in the drainages.

The large forest had more steep slope than the other two sites which were dominated by moderate slope ($\chi^2 = 243$, df = 4, $P \ll 0.001$). Ashland also had more secondary drainages and Fulton had fewer than expected ($\chi^2 = 21.12$, df = 4, $P < 0.001$). Millersburg was intermediate between Ashland and Fulton in all three drainage categories (Fig. 5).

Differences in amount of forest edge among the three forests were striking but not surprising considering the clearcuts at Millersburg. Over 40% of the Millersburg blocks included forest edge while fewer than 10% of the blocks at Ashland and Fulton contained forest edge (Fig. 5). The Chi-squared value for edge is the highest of the four variables considered and thus is a major source of variation among the three forests ($\chi^2 = 368$, df = 6, $P \ll 0.001$).

Each species occupied areas with statistically similar topographic features in each year of the study period (χ^2 tests, all $P > 0.1$). For further analyses we used only the data from 1988 which had the most thorough censuses. The best fit log-linear models were quite different for the three species but included all variables. These models suggest that they do not choose territory sites randomly with respect to the four variables considered and that the three species choose different topographic features.

The model for Worm-eating Warbler (S + D + E + L; df = 18, $G^2 = 16.93$, $P = 0.425$) shows that each of the four variables is independent of the others. This species avoided edge and preferred steep, lower slopes that were near small streams.

The model for Ovenbirds (ALD + AS + AE + LS + SD; df = 47, $G^2 = 32.55$, $P = 0.836$) included three interaction terms with the study area variable, indicating that this species did not choose the same topographic features at all three

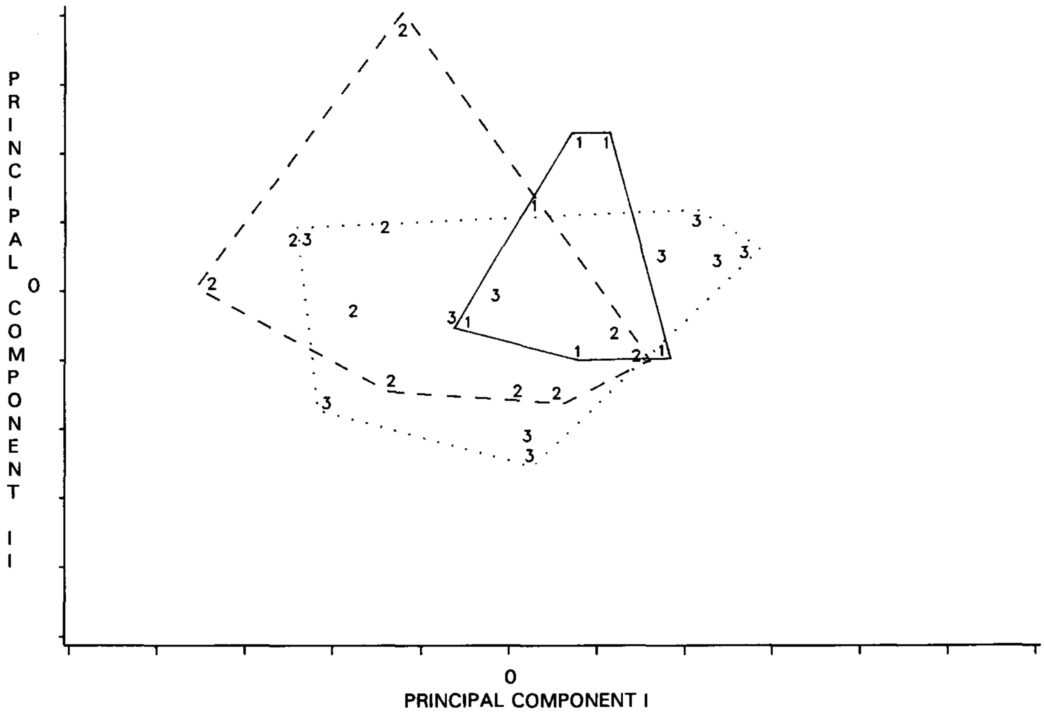


FIGURE 4. Principal component analysis of vegetative features of Kentucky Warbler territories at Ashland (1), Millersburg (2), and Fulton (3).

sites. Ovenbird territories included forest edge more frequently at Millersburg than at the other two sites. Similarly, flat areas were chosen more often at Ashland than at Millersburg. Overall, they preferred upland and higher slope areas with moderate slope, no streams, and no edge.

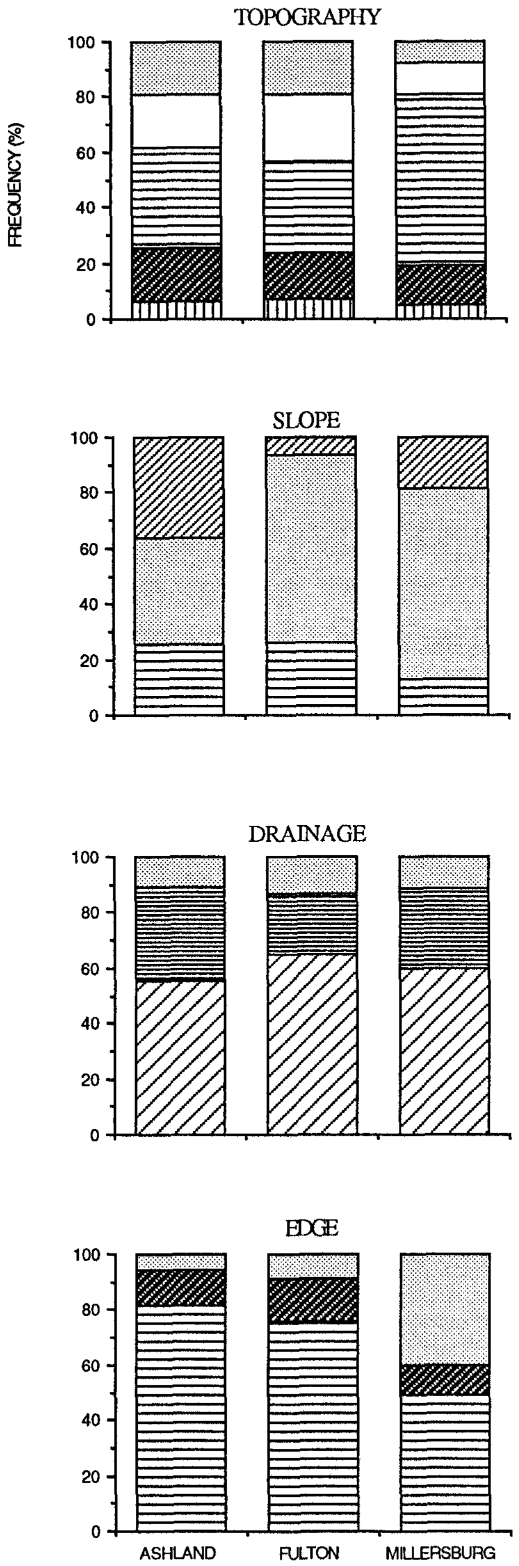
Kentucky Warblers preferred bottomland and lower slope locations with primary streams and riparian edge. They exhibited no preference for the steepness of slope at any of the three forests. Kentucky Warblers had the most complex model (ALE + ADE + ALD + ASE + LDE + LSD; df = 12, $G^2 = 15.46$, $P = 0.217$) with four of the six interaction terms including the study area variable. Edge, drainage and topographic location also appeared in four of the six terms. The complexity of this model and the relatively low P-value compared with the model and P-value for Ovenbirds suggest that the variables measured more adequately described Ovenbird territories than those of Kentucky Warblers.

Edge effect. Kentucky Warblers showed no consistent trend in relative density with increasing distance from edge, although they showed a tendency to have lower density in areas where Ovenbirds had high density (Fig. 6). At Millersburg, Kentucky Warbler density was significantly lower in the edge and center bands than in the band 200–300 m from the edge ($F = 3.7$, df = 3, 12, $P < 0.05$). Density at Fulton showed an opposite but non-significant pattern ($F = 1.7$, df = 4, 15, $P > 0.10$). Ovenbirds had significantly higher density beyond 200 m from the edge of the forest than within 100 m of the edge at both Millersburg ($F = 4.0$, df = 3, 12, $P < 0.05$) and Fulton ($F = 4.2$, df = 4, 15, $P < 0.025$).

DISCUSSION

CAUSES OF REDUCED DENSITY IN FRAGMENTS

Why are densities lower in the 300 ha forests than in the large forest, despite the presence of apparently abundant suitable habitat in all forests? We found no significant differences between structural characteristics of the vegetation among the three forests, which suggests that habitat quality is not limiting. Suitable habitat for Worm-



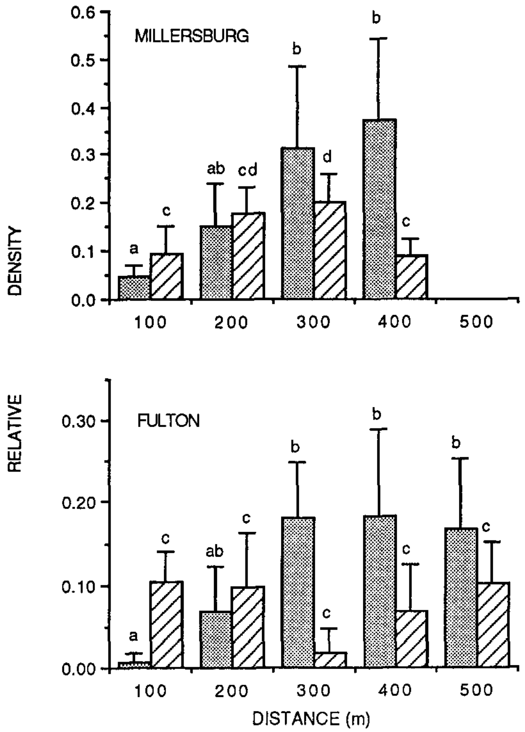


FIGURE 6. Relative density of Kentucky Warblers (striped bars) and Ovenbirds (shaded bars) at increasing distance from the forest edge at Millersburg (above) and Fulton (below). Relative density is defined as the proportion of each 100 m wide band occupied by each species. The numbers of the x-axis refer to the inner boundary of a 100 m wide band. For example the first band is from 0–100 m from the edge, the second band from 100–200 m and so on. Within each species, points with the same letter superscripts are not significantly different at the 5% level.

eating Warblers, however, usually is described as including steep slopes (Bent 1953, Kahl et al. 1985, Greenberg 1987). While some apparently suitable Worm-eating Warbler habitat does exist at Fulton (the isolated site where the species was

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FIGURE 5. Habitat characteristics of the three study sites with respect to four variables. For each of the four variables, the y-axis shows the proportion of each study area comprised of each category. Topography includes upland sites (shaded), upper slopes (white), intermediate slopes (horizontal bars), lower slopes (diagonal bars), and bottomland sites (vertical bars). Slope includes steep (diagonal bars), moderate (shaded), and flat (horizontal bars) categories. Drainage refers to primary streams (shaded), secondary streams (horizontal bars), and no streams (diagonal bars). Edge categories include forest edge (shaded), stream edge (diagonal bars), and forest interior (horizontal bars).

recorded) there is significantly more forested steep slope habitat at Ashland (Fig. 5). Furthermore, most of the slope areas at Fulton are within 100 m of the forest edge, which may decrease the suitability of this site for breeding by Worm-eating Warblers. Preferences by the other two species are not as specific (Fig. 2) (Collins 1983, Robinson 1992).

One explanation for the observed lower densities is that these forest interior species suffer from increased levels of brood parasitism by Brown-headed Cowbirds and nest predation associated with the higher proportion of forest edge in fragments than in larger forests (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Burger 1988). Our results suggest that Ovenbirds but not Kentucky Warblers are negatively affected by forest edge (Fig. 6). This difference in sensitivity to edge could explain the higher population sizes of Kentucky Warblers compared to Ovenbirds on the two isolated sites (Table 1). Ovenbirds forage on the ground for leaf litter insects (Bent 1953, Stenger 1958, Holmes et al. 1979), which may be more susceptible to dessication and thus less abundant closer to the forest edge (Gibbs 1988, Robinson 1992) compared to insects of dense foliage favored by Kentucky Warblers (Smith and Shugart 1987, this study). Thus, for Ovenbirds a square forest fragment of 1 square kilometer (100 ha) would have an effective area of 64 ha with an edge effect of 100 m and only 36 ha with an edge effect of 200 m. The apparent negative effect of edge on Ovenbirds could explain their absence from the northernmost portion of Millersburg, because it was relatively long and thin with a maximum width of 200 m. This area may have been functionally all edge for Ovenbirds.

Other non-edge habitat features also could influence population density. While vegetation was similar in all three forests (Fig. 1), the topography was quite different (Fig. 5). It is likely that both of these aspects of habitat are important in different combinations for each species. The main result of the analysis of topographic features was that the characteristics of Ovenbird and Kentucky Warbler territories differed among forests. It is not clear from our study whether these birds accept poorer quality habitat in fragments; additional sites need to be studied.

Population-wide patterns of dispersal and survivorship also may help explain differences in population density among forests. On local scale (i.e., Boone and Callaway counties), the fragments are much more isolated from other large forests compared to the Ashland site. On a regional scale, all three sites are peripheral to the majority of forest in Missouri (Giessman et al. 1986). The study sites are located towards the northwestern limit of the geographic ranges of Kentucky and Worm-eating Warblers and the southwestern limit of Ovenbirds (Emlen et al. 1986, Robbins et al. 1986). The three sites probably receive fewer immigrants than forests in the more central portions of the species' ranges. Among the study sites, Ashland probably receives more immigrants than the fragments because it is contiguous with extensive forest. Furthermore, Ashland is connected with forest along the Missouri and Mississippi Rivers, which are major routes for spring migrants. Thus, Ashland may be buffered from demographic fluctuations.

Lower immigration than emigration is a widely accepted but difficult-to-demonstrate explanation for low populations in small fragments (Leck et al. 1988, Robinson 1992). It is clear, however, that the small numbers of breeding individuals of these species (Gibbs and Faaborg 1990) and high nest predation (Burger 1988) in the forest fragments result in very few offspring available to recolonize these fragments or sites near them.

MINIMUM AREA REQUIREMENTS

Our results are in general agreement with other studies that have found higher population densities of forest-interior species in larger forest fragments than in smaller fragments (Whitcomb et al. 1981, Ambuel and Temple 1983, Lynch and Whigham 1984, Askins et al. 1987). The limitations of the incidence function are most clearly demonstrated with our data on Worm-eating Warblers (Table 1). This species was not present at the 300 ha site and was present but not breeding at the 340 ha site which suggests that larger forests are required by this species. In addition, steep slopes in the forest interior are important for suitable Worm-eating Warbler habitat. A minimum area requirement of one-half the size at maximum occurrence, as suggested by Robbins et al. (1989a), would certainly be too small for this species in Missouri.

For Ovenbirds and Kentucky Warblers the suitability of 300 ha forests depends on how a minimum viable population is defined and the validity of applying the MVP concept to populations in forest fragments. An effective population size of 50 is frequently mentioned as an estimate of minimum viable population size (Franklin 1980, Soule 1980). While the time-intensive census techniques we used restricted us to only three sites, our results suggest that the incidence function may underestimate the minimum area required for an effective population size of 50. Note in Table 1 that the number of breeding pairs in the small forests range from five to 26. Because effective population sizes usually are lower than the actual number of individuals (Franklin 1980), the populations of Ovenbirds and Kentucky Warblers probably are lower than the theorectical MVP of 50.

To refine estimates of minimum area requirements, the reproductive parameters of the populations need to be considered along with habitat characteristics. Factors that affect breeding success of insectivorous, forest interior, ground-nesting warblers in our central Missouri study sites include nest predation (Burger 1988) and male-biased sex ratios (Gibbs and Faaborg 1990). These two factors contribute to considerably reduced breeding populations even in the relatively large forest fragments of 300 ha.

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