PATTERNS OF OVENBIRD (*SEIURUS AUROCAPILLUS*) PAIRING SUCCESS IN MISSOURI FOREST TRACTS

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ABSTRACT.—Minimum-area-requirement estimates for area-sensitive birds may underestimate the actual area needed to provide long-term breeding habitat because they do not consider the pairing and mating success of territorial males. Patterns of pairing success were studied in Ovenbirds (*Seiurus aurocapillus*) in north-central Missouri in forest tracts below, approaching, and exceeding minimum-area-requirement estimates for this species. The possible roles of habitat area, isolation, and edge effect in causing reduced pairing success were examined. Male Ovenbird territories were spot mapped within seven forest tracts. Each male was observed to determine if he had acquired a mate. The percentage of paired male Ovenbirds was directly related to forest-tract area and total estimated male Ovenbird population. A higher percentage of males with territories more than 300 m from the forest edge were paired than males with territories less than or equal to 300 m from the forest edge. The combined effect of total forest area, edge-to-interior ratio, and percent forest cover within a 5-km radius of the tracts was highly correlated with pairing success. Edge effects are an important consideration that should be a contributing factor when developing minimum-area-requirement estimates. *Received 9 June 1993, accepted 24 October 1993.*

STUDIES OF THE RESPONSES of area-sensitive birds to forest fragmentation often focus on the question of quantifying minimum-habitat-area requirements for these species (Galli et al. 1976, Blake 1983, Hayden et al. 1985, Robbins et al. 1989). Minimum-area requirements are estimated by: (1) the minimum area of occurrence (Galli et al. 1976, Blake 1983, Hayden et al. 1985); (2) the inflection point of species-specific incidence functions (Diamond 1978, Robbins 1979); and (3) logistic regression examining the relationship between forest area and the probability of detecting a species (Robbins et al. 1989).

Designs of nature reserves based on these estimates are discouraged for a variety of reasons (Robbins 1979, Whitcomb et al. 1981). For example, male Kirtland's Warblers (*Dendroica kirtlandii*) occupying marginal habitat experience lower pairing success than males in optimal habitat (Probst and Hayes 1987). Breeding birds within suggested minimum-area tracts also may suffer greater rates of nest predation (Wilcove 1985, Burger 1988), brood parasitism (Brittingham and Temple 1983, Robinson 1992) and, hence, lower nesting success when compared with cohorts within forest tracts larger than the minimum-area requirement.

A valid estimate of the minimum-area requirement for a site would require detailed demographic data for the species involved at the site plus information on the exchange of individuals between sites within the metapopulation (Schaffer 1981). Such data would determine which locations support "source" populations and which are "sinks" (Pulliam 1988), regularly being "rescued" by colonization from sources (Brown and Kodric-Brown 1977). Information on this critical management issue currently is not available.

Our studies have focused on population characteristics of area-sensitive forest wood-warblers in tracts below, approaching, and exceeding the 340-ha estimated minimum-area requirement for a given species in central Missouri (Hayden et al. 1985). Despite comparable habitat availability in two 300-ha forest fragments and a 900-ha control site (Wenny et al. 1993), we found populations of the Kentucky Warbler (*Oporornis formosus*) and Ovenbird (*Seiurus aurocapillus*) were about one-half as dense in the fragments (Wenny 1989). Additionally, pairing success of the Ovenbird was greatly reduced on the fragments when compared to sites

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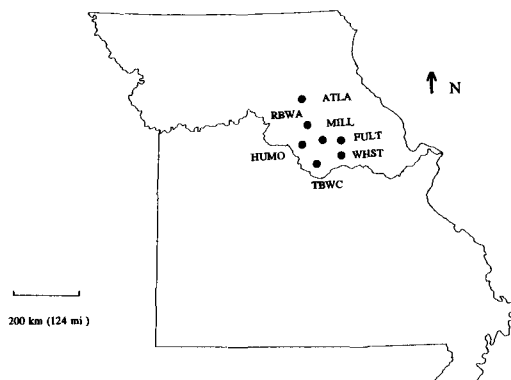[2] Present address: 323 Center St., Suite 200, Little Rock Arkansas 72201, USA.

Fig. 1. Locations of study sites in Missouri.

TABLE 1. Characteristics of study sites.

Site name (acronym)	Total area (ha)	Percent forested land within 5 km	Edge-to-area ratio
Atlanta Wildlife Area (ATLA)	350	23	1.30
Thomas Baskett Wildlife Center (TBWC)	900	80	0.10
Rudolph Bennitt Wildlife Area (RBWA)	900	52	0.32
Fulton (FULT)	300	18	0.40
Hungry Mother (HUMO)	150	46	0.53
Millersburg (MILL)	300	20	0.79
Whetstone Creek (WHST)	350	31	1.60

exceeding the minimum-area requirement (Gibbs and Faaborg 1990). Overall, these 300-ha forest fragments contained about 20 singing male Ovenbirds, but actually supported as few as seven breeding pairs each.

In this paper, we examine further the patterns of pairing success in isolated populations of the Ovenbird within forests in central Missouri. The possible roles of habitat area, isolation, and edge effect in causing reduced pairing success were evaluated. First, we examined pairing success rates among a number of forest fragments supporting Ovenbird populations of varying size, and then we evaluated pairing success in relation to territory location within two large forests (900 ha).

METHODS

Study areas.—Each study site was once part of a single extensive forest, interdigitated with fingers of prairie located along the Missouri and Chariton rivers. This presettlement forest once covered 77% of the five counties containing the study sites. Following settlement, this once extensive forest was extremely reduced in area and fragmented. Today, forest cover within the five-county area exists as 3,960 fragments covering 23% of the land area (Giessman et al. 1986).

County road maps with satellite overlays of forest cover (compiled by the Missouri Department of Conservation) and a listing of forest tracts by county and size (Giessman et al. 1986) were evaluated for tracts 150-ha or larger in counties north of the Missouri River. During the 1988-1989 pilot season, 39 forest tracts within the Chariton River valley and adjacent areas were censused for Ovenbirds. Of these, seven sites were selected as suitable study sites because of accessibility, and contrasting differences in forest area, total number of male Ovenbirds, edge-to-area ratios, and relative isolation from other forest tracts (mea-

sured as amount of forest cover within 5-km radius of each forested area; Fig. 1, Table 1). The edge-to-interior ratio was calculated for each tract by laying a grid, calibrated in 0.25-ha blocks, over topographic maps of each study area. The number of 0.25-ha blocks containing edge was divided by the total number of forested blocks to calculate the edge-to-interior ratio (Table 1).

We collected data from two large forests and five forest fragments. The two large forests include: Thomas S. Baskett Wildlife Research and Education Center (TBWC) located in Boone County, Missouri; and Rudolph Bennitt Wildlife Area (RBWA) located in Boone, Randolph, and Howard counties, Missouri (Fig. 1). The TBWC encompasses about 900 ha and is contiguous with forest tracts to the south and east. The RBWA contains about 900 ha of forest cover and is surrounded by agricultural land. The vegetation on both sites was composed of mature, upland, secondary forest dominated by oak (*Quercus* sp.) and hickory (*Carya* sp.). The understory plant community consisted of flowering dogwood (*Cornus florida*), viburnum (*Viburnum* sp.), hophornbeam (*Ostrya virginiana*), serviceberry (*Amelanchier arborea*) and sugar maple (*Acer saccharinum*). Ground cover included aromatic sumac (*Rhus aromatica*), Virginia creeper (*Parthenicissus* sp.), buck brush (*Symphoricarpos orbiculatus*), and poison ivy (*Toxicodendron radicans*).

The five smaller fragments were similar in vegetative composition to that of the TBWC and RBWA sites (Gentry 1989, Seng 1990). The Millersburg (MILL) and Fulton (FULT) tracts (both 300 ha), as well as the Whetstone Creek Wildlife Area (WHST; 350 ha), are located in Callaway County, Missouri (Fig. 1). The Hungry Mother Wildlife Area (HUMO; 150 ha) is in Howard County, and the Atlanta Wildlife Area (ATLA; 350 ha) is located in Macon County (Fig. 1).

Evaluating pairing success within forest fragments of varying size.—Territory locations of singing male Ov-

enbirds were delineated using the spot-mapping technique from April through June 1989 (International Bird Census Committee 1970). Spot mapping was conducted from sunrise to 4 h after sunrise to delineate territory locations. Plots of approximately 150 ha within ATLA, TBWC, RBWA, and WHST were censused by walking systematically through each plot (Table 1). The plot size of 150 ha was chosen because it is large enough to contain several Ovenbird territories. In the smaller tracts (MILL, FULT and HUMO), plots were not used because it was feasible to census the entire tract. Plots were rectangular and placed where Ovenbirds were known to occur. All plots included interior forest and external edge portions. Interior edges created by forest-management practices were avoided.

We visited each site four to five times in sequential order so that visits were spaced evenly throughout the field season. Territories of male Ovenbirds were defined as clusters of two or more registrations from different visits. Two registrations can be used to delineate a territory if a minimum of five site visits are made (International Bird Census Committee 1970). We did not have time to visit each tract five times because of the number of fragments involved and the short duration breeding season; however, all fragments were visited at least four times. Countersinging events were used to help delineate territory boundaries.

To assess paired status, we recorded the number of songs given by each territorial male during a 5-min period. We considered birds paired if they sang six or fewer times during the 5-min sample. Gibbs (1988) derived these criteria from extensive field studies that were later replicated by Gentry (1989) and confirmed by Van Horn (1990). Males were evaluated for paired status at each visit unless call-back tapes were used.

The singing rate, especially for mated birds, changes at different stages of the breeding cycle (Kroodsma et al. 1989). Because paired birds sing so infrequently, we occasionally used playback tapes to enhance detection of paired birds. We did not conduct song-rate counts on birds that responded to the tape. Additionally, we only considered a male paired when it had a low singing rate and was observed with a mate or carrying food. Conversely, we considered birds unpaired if they had a high singing rate and the behaviors listed above were not observed.

Because unpaired males sing more often than paired males, we may have detected more unpaired males, but this potential bias is consistent throughout all study sites. It is generally assumed that most migratory passerines are unpaired upon arrival at the breeding grounds, and detectabilities at this time are similar (Pettingill 1985). Furthermore, as the season progressed, use of tape-recorded calls ensured detectability of paired males that did not sing as often.

We did not distinguish between territories of males that remained on the territory for the entire breeding season and males that may have abandoned the territory in search of another mate or territory location. It is possible that such movements could create an inflated sample of unpaired males; however, this sampling artifact is unlikely in this study because males (paired or unpaired) were included in the analysis only if enough registrations were recorded to delineate the territory.

Ovenbird density data collected within 150-ha census plots were multiplied by the area of each tract to estimate population size for each tract. The calculation of total population size assumes that density remained constant throughout each study area. Because Ovenbird territory density may not be constant throughout a forest tract (Gentry 1989) and because forest habitat quality within a tract is not uniform (Van Horn 1990), the total male Ovenbird population estimates may be exaggerated. Pearson product-moment correlations were used to determine if the total male Ovenbird population size within a forest tract was related to the percent paired male Ovenbirds and/or density of territorial males.

Simple regressions were used to determine if total forest area could predict percent paired male Ovenbirds. A multiple-regression analysis was computed to determine the relative importance of area, edge and local isolation of forest tracts on pairing success of Ovenbird populations (Sokal and Rohlf 1981, SAS Institute 1985a, b).

Pairing success in relation to edge in large forests.— Ovenbirds were spot mapped using the same method described above from 7 May through 30 June 1989 on TBWC, and from 23 April through 15 June 1990 on TBWC and RBWA. Three management units totalling about 110 ha on TBWC and 133 ha on RBWA were spot mapped. Each area censused included forest interior and external forest edge. A territory was delineated if a singing male was detected at least eight times in the same area during 10 to 12 site visits. Countersinging males were used in delineating territories. The paired status of each male was determined using the singing-rate-index technique and visual confirmations of breeding activity described earlier. Because more site visits were made in this portion of the study, we were able, for some males, to document shifts in paired status from unpaired to paired. These males were considered paired for analysis purposes.

We defined edge habitat as the boundary between grassland (or pasture) and forest. Each territory was placed in one of six 100-m distance classes according to the distance of the center of the territory from the forest edge. We selected 100-m distance classes because these intervals were wide enough to encompass Ovenbird territories in north central Missouri (Wenny 1989). The last distance class (501–600+ m) included a few territories greater than 600 m from the forest edge. We were unable to form a 601- to 700-m distance class because there were few locations within

each forest greater than 600 m from an exterior forest edge or interior clearcuts.

To determine if the pairing success of male Ovenbirds was related to the distance of the territory from the forest edge we used Williams' corrected G-tests of independence to compare the ratio of paired to unpaired birds in each distance class. We tested the association between pairing success and distance of the territory from the forest edge using Spearman rank correlations. Distance classes were pooled into the two most meaningful groups for comparison. G-tests of heterogeneity were used to determine how to pool the distance classes into the two most meaningful groups for comparison (Sokal and Rohlf 1981, SAS Institute 1985a, b). The proportion of paired to unpaired birds between these pooled distance classes was tested.

Habitat measurements.—To assess influences of habitat quality on pairing success, we measured eight habitat variables considered important in describing Ovenbird habitat in Missouri (Sweeny and Dijak 1985, Wenny 1989) and Minnesota (Collins et al. 1982): basal area, slope, canopy height, litter depth, percent canopy closure, percent ground cover, shrub density, and shrub height. All vegetation measurements were completed during early to mid-July 1990. Six of the eight variables measured do not change significantly between April (when the birds are establishing territories) and July (when variables were measured). Values for percent canopy closure and percent ground cover measured in July would differ from conditions present in April. However, these parameters are important in characterizing forest structure and reflect habitat conditions that Ovenbirds are likely to assess in the spring.

Measurements for slope, percent canopy closure, percent ground cover, and shrub density were collected using techniques described by James and Shugart (1970). Techniques used for the remaining parameters are modifications of this standard method and are discussed below. Vegetation measurements were collected from four, 0.4-ha circular plots located within each territory. Locations of circular plots were randomly selected within each territory and established using the centroid of the territory as a reference point. At the center of each plot, a meter stick was used to measure shrub height and litter depth. A clinometer was used to estimate tree height and slope. We used a 10-factor prism to estimate the basal area for each plot (Hovind and Rieck 1970). Use of a prism permitted timely collection of basal-area data but, because it is a plotless method, additional trees outside of the plot may have been included in the basal-area calculation. We think this method provides a reasonable estimate of the basal area within each territory, and any error in the measurement is consistent across all territories.

A two-level nested ANOVA was conducted on each vegetation parameter to test for differences between territories of paired and unpaired birds at each study site (Sokal and Rohlf 1981, SAS Institute 1985a, b). To meet the assumptions of such an analysis, data values for total stems per hectare were transformed to a lognormal distribution. Stepwise discriminant analysis and discriminant-function analysis (SAS Institute 1985a, b) were used to evaluate the importance of each parameter simultaneously. Correlations of parameters included in these analyses were evaluated.

The stepwise discriminant analysis was conducted using distance as a variable in addition to the vegetation parameters to determine what variables were most important in distinguishing between the territories of paired and unpaired birds. In the discriminant-function analysis, we included variables in the function that were significant in the ANOVA and those shown to be most important in the stepwise discriminant analysis. We then eliminated parameters one at a time to determine how much they contributed to classifying birds as paired or unpaired. If the parameter made no contribution, we eliminated it from the function. We also conducted separate discriminant-function analyses using each habitat variable individually to see how accurately each parameter could classify birds as paired or unpaired.

RESULTS

Pairing success within forests of varying size.— Ovenbird densities within TBWC (900 ha), Fulton (300 ha) and Millersburg (300 ha) sites were similar to density estimates derived from previous studies of these areas (Gibbs 1988, Wenny 1989). Estimated total number of male Ovenbirds for the study sites ranged from about 9 on a 350-ha tract to 125 on the 900-ha tracts (Table 2). The percent paired male Ovenbirds on study plots ranged from 0 on the smaller fragments (350 ha) to about 65 in the larger contiguous forests (900 ha).

Pearson product-moment correlations were computed for percent paired males within plots, density of territorial males, and total male Ovenbird population estimates for the forest tracts. As total male Ovenbird population estimates increased so did percent paired males within plots ($R^2 = 0.923$, $P < 0.01$). However, male densities from plots were not correlated with percent paired male Ovenbirds within plots, or total male Ovenbird population estimates within forest tracts.

Percent paired males within plots also was correlated with forest area and estimated total MOB population ($R^2 = 0.795$, $P < 0.05$ and $R^2 = 0.923$, $P < 0.05$, respectively; Figs. 2 and 3). A multiple regression of these factors revealed

TABLE 2. Densities of territorial male Ovenbirds and numbers of breeding pairs within survey plots, and estimates of total male population on seven forested tracts in north-central Missouri in 1989.

Site[a]	Area censused (ha)	Density within plots[b]	Males within plots			Estimated total no. males per ha
			Paired	Unpaired	Percent paired	
ATLA	211	0.83	3	12	20.0	0.08
FULT	157	0.59	1	7	12.5	0.06
HUMO	100	1.96	5	13	27.7	0.20
MILL	160	0.45	1	5	16.6	0.05
RBWA	180	1.38	9	11	45.0	0.14
TBWC	167	1.41	13	7	65.0	0.14
WHST	224	0.26	0	5	0.0	0.03

[a] See Table 1 for site names.
[b] Number of males/10 ha.

that the combined effect of total male Ovenbird population within a forest tract and forest area were significantly correlated with percent paired males ($R^2 = 0.920$, $P < 0.05$).

A multiple regression of total forest area, edge-to-interior ratio, percent forest cover within a 5-km radius of each tract, and pairing success did not reveal which of the three habitat factors contributed most to pairing success. However, the combined effect of these factors was highly correlated with pairing success ($R^2 = 0.884$, $P < 0.01$).

Patterns of pairing success within large forests.— Comparisons of the proportion of territories with paired and unpaired birds among distance intervals from the forest edge were made for each year within the two large sites (Table 3). Pairing success was related to the distance of the territory from the forest edge ($P = 0.005$ in 1990 at TBWC and RBWA). A similar but non-significant trend ($P > 0.05$) was apparent at TBWC in 1989.

The percentage of paired male Ovenbirds was positively correlated with increasing distance of the territory from the forest edge in 1990 at RBWA ($R^2 = 0.800$, $P = 0.05$) and TBWC ($R^2 = 0.830$, $P = 0.04$). The correlation for TBWC in 1989 was not significant, but the results imply a similar direct positive relationship between percent paired male Ovenbirds and distance of the territory from the forest edge ($R^2 = 0.540$, $P = 0.54$). For TBWC and RBWA in 1990, but not TBWC in 1989, there were more paired males with territories more than 300 m from the forest edge than males occupying territories 300 m or closer to the forest edge (Table 3).

Four vegetation parameters differed between territories with paired and unpaired male Ovenbirds, but these differences were not consistent between RBWA and TBWC (Table 4). Mean tree height, litter depth, and canopy cover were greater in territories with paired birds than for those with unpaired birds ($P = 0.01$, 0.02 and 0.002, respectively) at RBWA. At TBWC mean tree height and litter depth were higher in territories of paired birds ($P < 0.001$ and 0.01, re-
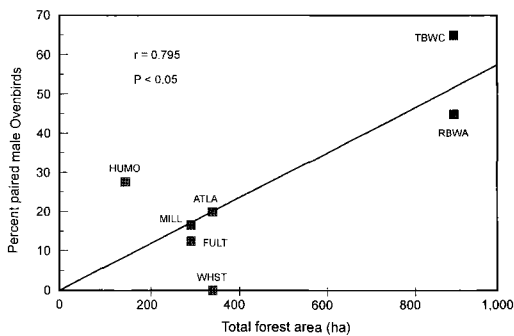

Fig. 2. Relationship between percent paired male Ovenbirds and forest area in north-central Missouri, 1989.
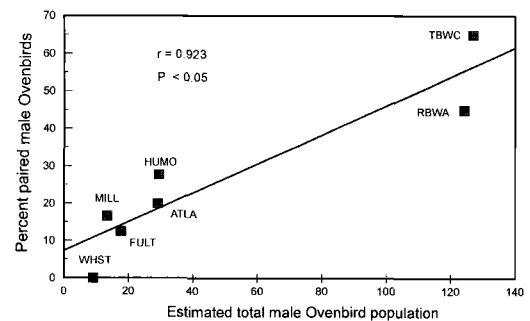

Fig. 3. Relationship between percent paired male Ovenbirds and total male Ovenbird population by forest tract in north-central Missouri, 1989.

TABLE 3. Williams' corrected G-tests of independence comparing proportion of paired and unpaired male Ovenbirds with territories in each distance class, and G-test of heterogeneity comparing proportion of paired to unpaired male Ovenbirds among pooled distance classes for Thomas S. Baskett Wildlife and Research Center (TBWC) for 1989 and 1990, and Rudolph Bennitt Wildlife Area (RBWA) for 1990.

Distance class	TBWC 1989		TBWC 1990		RBWA 1990	
	Paired	Unpaired	Paired	Unpaired	Paired	Unpaired
0–100	1	6	0	3	0	7
101–200	2	7	2	5	2	9
201–300	4	2	0	1	2	7
301–400	0	3	6	0	2	0
401–500	2	3	3	0	4	0
501–600	3	1	5	0	3	2
G_{adj}	8.85		20.86		19.23	
P	>0.1		<0.005		<0.005	
Pooled classes						
0–300	7	15	2	9	4	23
301–600	5	7	14	0	9	2
G	0.34		22.24		15.74	
P	>0.1		<0.005		<0.005	

spectively), whereas percent ground cover was less ($P = 0.006$). No significant correlations were found between pairs of these habitat variables.

A stepwise discriminant analysis was used to determine which habitat structure parameters could best describe the variation between paired and unpaired males. The distance of territories from the forest edge explained 58% of the variation ($P < 0.001$), while ground cover accounted for 21% ($P = 0.03$) between territories of paired and unpaired males at TBWC. On RBWA, the distance of territories from the forest edge accounted for 38% ($P < 0.001$) and slope for 13% ($P = 0.03$) of the variation between paired and unpaired male territories.

To determine how accurately distance of the territory from the forest edge and other habitat

variables could predict paired or unpaired Ovenbird status, we conducted discriminant analyses. For RBWA a single variable, distance of the territory from the forest edge, was 69% accurate in classifying males as paired and 87% accurate in classifying males as unpaired. The classification accuracy could not be improved by adding any vegetation parameter to the discriminant function or by using any single vegetation parameter. A similar trend was demonstrated at TBWC, with distance of the territory from the forest edge achieving 87% accuracy in classifying males as paired and 100% accuracy in classifying males as unpaired. However, the accuracy of this classification was 100% for paired and unpaired males when percent ground cover was added to the function. None

TABLE 4. Comparisons of vegetation values ($\bar{x} \pm$ SD) for territories of paired and unpaired Ovenbirds for Thomas S. Baskett Wildlife and Research Center (TBWC) and Rudolph Bennitt Wildlife Area (RBWA) for 1990 using two-level nested ANOVA.

	TBWC			RBWA		
	Paired ($n = 18$)	Unpaired ($n = 9$)	P	Paired ($n = 13$)	Unpaired ($n = 24$)	P
Slope	12.4 ± 3.2	11.4 ± 3.5	0.3	15.6 ± 6.5	13.3 ± 6.3	0.1
Tree height (m)	22.9 ± 3.8	18.2 ± 4.6	<0.001	21.6 ± 5.3	18.4 ± 4.9	0.01
Litter depth (cm)	3.0 ± 1.3	2.2 ± 1.1	0.01	3.6 ± 1.9	2.9 ± 1.3	0.02
Percent canopy closure	87.7 ± 8.1	88.5 ± 8.2	0.7	81.8 ± 9.8	72.6 ± 15.2	0.002
Percent ground cover	20.5 ± 15.7	42.1 ± 24.0	0.006	55.7 ± 17.2	53.0 ± 21.7	0.6
Shrub height (cm)	33.4 ± 14.3	40.7 ± 17.9	0.1	60.9 ± 20.4	58.1 ± 26.8	0.7
Stem density/ha[a]	3.4 ± 0.3	3.4 ± 0.3	0.9	3.7 ± 0.2	3.7 ± 0.5	0.7
Basal area	110.1 ± 27.2	104.2 ± 26.8	0.4	85.2 ± 28.5	86.3 ± 25.8	0.8

[a] Log-transformed values.

of the other variables could individually classify birds as paired or unpaired as accurately as distance of the territory from the forest edge.

DISCUSSION

These data demonstrate that the percentage of paired male Ovenbirds from forests in north-central Missouri is directly related to both contiguous forest area and total male Ovenbird population size, and positively influenced by territory placement more than 300 m from the forest edge.

Pairing success of male Ovenbirds within large forest tracts for the TBWC 1990, and RBWA datasets increased beyond 300 m of the forest edge. The TBWC 1989 data, while showing a similar trend, were not significant. The pattern exhibited by the TBWC 1989 data is likely a result of our initiation of censusing after most pair bonds had formed. In spite of induced countersinging through use of the playback tapes, it is likely that we were unable to locate territories of paired males because the singing rate drops significantly after pair bonds are formed.

Previous work in north-central Missouri suggested that Ovenbird populations in fragmented forests contained a greater proportion of unpaired males than found in larger forests (Gibbs and Faaborg 1990). The patterns observed in our study are complementary to these previous findings. We do not know if this accurately reflects populationwide sex ratios or may be a result of sexual differences in dispersal. However, we hypothesize that the apparent excess of unpaired males may be the result of territory establishment in edge habitat. Females may choose to avoid males defending edge territories. Alternatively, females may pair with these males, but subsequently be depredated or forced to abandon the territory as a result of negative influences of edge. It is unknown if males with territories in edges pair later than those in the interior. Future research on sex ratios, dispersal, and male/female interactions near forest edge is needed throughout the Ovenbird breeding range to characterize this pattern in greater detail.

Although other studies have shown reduced nesting success by Ovenbirds on forest fragments (Wander 1985, Porneluzi et al. 1993, M. A. Villard unpub. data), they did not show the aversion to edge shown here. We suggest that this may reflect the history of north-central Missouri, as this region was once a very heterogeneous blend of forest and prairie. Ovenbirds living in this region in presettlement times may have dealt with higher nest predation (Wilcove 1985, Burger 1988) or cowbird parasitism rates (Brittingham and Temple 1983, Robinson 1992) associated with forest edge. As a result, behaviors that result in avoidance of edge may have evolved. In the more uniformly forested regions to the east, such behavior would have been maladaptive, as it would have excluded extensive tracts of suitable nesting habitat from consideration.

Correlations from our study indicate that total male Ovenbird population is more closely related to pairing success than male Ovenbird density. We hypothesize that total male Ovenbird population is a function of forest area, whereas male Ovenbird density is a function of habitat quality. If so, small high-quality fragments would have high density and low pairing success in comparison to large contiguous tracts. These fragments also should have higher pairing success than fragments of comparable size with lower habitat quality. The Hungry Mother study area (at 150 ha) was the smallest tract studied, but it had the highest male Ovenbird density of all sites. However, this site ranked third (below the two large forests; 900 ha) in percent of paired male Ovenbirds. The high density at this site could be explained by the tract's low edge-to-interior ratio, and lowest isolation value compared to the other fragments. Conversely, our large study sites (900 ha) ranked highest in percent paired male Ovenbirds and contained at least four times the total male Ovenbird population than the fragments. An interesting follow-up study might consider how many, if any, males from neighboring fragments eventually claim territories on large contiguous forest tracts nearby.

Data from our study indicate that calculations of the minimum-area requirement for this species should focus on core areas rather than the area of the entire forest tract. For example, in a square forest tract totalling 800 ha, 39% of the area is within 300 m of the forest edge. This leaves 480 ha of suitable "core" habitat for breeding, which is below recent estimations of the minimum-area requirement for this species in Maryland and adjacent states (Robbins et al. 1989). If the forests are irregular in shape or have many large openings, even less core area

remains. Only 20 to 30 of nearly 4,000 forest fragments in north-central Missouri offer habitat beyond 300 m from the forest edge (Faaborg unpub. data).

Preservation of large contiguous forest tracts for breeding is one of the most important factors contributing to the long-term population viability of Ovenbirds in north-central Missouri. However, where such habitat protection is not possible, smaller tracts with low edge-to-interior ratios and in close proximity to large forests (at or exceeding the minimum-area requirement for Ovenbirds in the region) will provide suitable breeding habitat for Ovenbirds. Such tracts cannot replace large contiguous forests necessary to sustain populations, but may provide additional productive breeding habitat to supplement local and regional population levels. Similar studies are needed throughout the breeding range of this species to further characterize patterns in pairing success and elucidate regional variations.

LITERATURE CITED

BLAKE, J. G. 1983. Ecological relationships of breeding birds in isolated forest patches in east-central Illinois. Ph.D. dissertation, Univ. Illinois, Urbana.

BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445–449.

BURGER, L. D. 1988. Relations between forest fragmentation and depredation of artificial nests in Missouri. M.A. thesis, Univ. Missouri, Columbia.

COLLINS, S. L., F. C. JAMES, AND P. G. RISSER. 1982. Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. Oikos 39:50–58.

DIAMOND, J. M. 1978. Critical areas for maintaining

viable populations of species. Pages 27–40 *in* The breakdown and restoration of ecosystems (M. N. Holdgate and M. J. Woodman, Eds.). Plenum Press, New York.

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

GENTRY, R. M. 1989. Variable mating success of the Ovenbird (*Seiurus aurocapillus*) within remnant forest tracts of central Missouri. M.A. thesis, Univ. Missouri, Columbia.

GIBBS, J. P. 1988. Forest fragmentation, mating success, and the singing behavior of the Ovenbird (*Seiurus aurocapillus*) and Kentucky warbler (*Oporornis formosus*) in central Missouri. M.A. thesis, Univ. Missouri, Columbia.

GIBBS, J. P., AND J. FAABORG. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conserv. Biol. 4:193–196.

GIESSMAN, N. F., T. W. BARNEY, T. C. HAITHCOAT, J. W. MYERS, AND R. MASSENGALE. 1986. Distribution of forest land in Missouri. Trans. Mo. Acad. Sci. 20:5–14.

HAYDEN, T. J., J. FAABORG, AND R. L. CLAWSON. 1985. Estimates of minimum area requirements for Missouri forest birds. Trans. Mo. Acad. Sci. 19:11–22.

HOVIND, H. J., AND C. E. RIECK. 1970. Basal area and point sampling: Interpretation and application. Wis. Dep. Nat. Resour. Bull. 23.

INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24:722–726.

JAMES, F. C., AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KROODSMA, D. E., R. C. BERESON, B. E. BYERS, AND E. MINEAR. 1989. Use of song types by the Chestnut-sided Warbler: Evidence for both intra- and inter-sexual functions. Can. J. Zool. 67:447–456.

PETTINGILL, O. S., JR. 1985. Ornithology in laboratory and field, 5th ed. Academic Press, Orlando, Florida.

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. Conserv. Biol. 7:618–622.

PROBST, J. R., AND J. P. HAYES. 1987. Pairing success of Kirtland's Warblers in marginal vs. suitable habitat. Auk 104:234–241.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652–661.

ROBBINS, C. S. 1979. Effect of forest fragmentation on bird populations. Pages 198–212 *in* Workshop proceedings: Management of northcentral and northeastern forests for nongame birds (R. M.

DeGraaf and K. E. Evans, Eds.). U.S. Forest Service Gen. Tech. Rep. NC-51.

ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildl. Monogr. 103.

ROBINSON, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

SAS INSTITUTE. 1985a. SAS users guide: Basics. SAS Institute, Inc., Cary, North Carolina.

SAS INSTITUTE. 1985b. SAS user's guide: Statistics. SAS Institute, Inc., Cary, North Carolina.

SENG, P. T. 1990. The evaluation of techniques for determining tree squirrel abundance and habitat suitability in central Missouri. M.S. thesis, Univ. Missouri, Columbia.

SCHAFFER, M. L. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Co., New York.

SWEENY, J. M., AND W. D. DIJAK. 1985. Ovenbird habitat capability model for an oak-hickory forest. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 39:430–438.

VAN HORN, M. A. 1990. The relationship between edge and the pairing success of the Ovenbird (Seiurus aurocapillus). M.A. thesis, Univ. Missouri, Columbia.

WANDER, S. A. 1985. Comparative breeding biology of the Ovenbird in large vs. fragmented forests: Implications for the conservation of Neotropical migrant birds. Ph.D. dissertation, Rutgers Univ., Piscataway, New Jersey.

WENNY, D. 1989. Population density and area requirements of three forest interior warblers in central Missouri. M.A. thesis, Univ. Missouri, Columbia.

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, B. L. WHITCOMB, M. K. KLIMKIEWICZ, D. BYSTRAK. 1981. Effects of forest fragmentation of avifauna of the eastern deciduous forest. Pages 125–205 in Forest island dynamics in man-dominated landscapes (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.

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