HABITAT FRAGMENTATION AND
PAIRING SUCCESS IN THE OVENBIRD
(*SEIURUS AUROCAPILLUS*)

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ABSTRACT.—In 1990 and 1991, we determined the proportion of Ovenbird (*Seiurus aurocapillus*) territorial males that were paired in a 25-ha plot in an extensive forest (>350 km²) in Québec, and compared it to pairing success in populations breeding in nearby forest fragments (4.5–53.0 ha) in Québec and Ontario. We tested the hypotheses that pairing success would increase with population density, and decrease with the degree of fragmentation of the habitat. Pairing success was higher in the extensive forest in both years, although the difference was only marginally significant ($P < 0.10$) in 1990 (82.4 vs. 58.6%), and not significant ($P > 0.25$) in 1991 (76.5 vs. 58.3%). The density of territorial males was twice as high in the extensive forest as in the forest fragments. When including data from similar studies conducted in New Jersey and Missouri, we found that pairing success increased and gradually levelled off with the density of territorial males. Although we lacked a common parameter for measuring habitat fragmentation across all three studies, pairing success appeared to decrease with the isolation of forest fragments from surrounding woodland, while it remained stable around 80% in extensive forests of all three studies. The effect of habitat fragmentation on pairing success was particularly severe in the Missouri study area, at the periphery of Ovenbird's breeding range. A general linear model showed that woodland configuration— the location of a study site in an extensive or fragmented forest—was the best predictor of pairing success, and that geographical location also had a significant effect. We conclude that habitat fragmentation reduces pairing success by altering dispersal dynamics or habitat selection by females. *Received 6 April 1992, accepted 17 November 1992.*

THE OVENBIRD (*Seiurus aurocapillus*) has been shown to be sensitive to the area of contiguous habitat in various parts of its breeding range (Bond 1957, Robbins 1979, Whitcomb et al. 1981, Hayden et al. 1985, Robbins et al. 1989, Villard 1991). Ovenbird abundance also has been found to decrease significantly with the isolation of a forest fragment from surrounding woodland (Whitcomb et al. 1981, Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989). Due to the apparently dominating effect of patch area—or the area of "core" habitat (Temple 1986)—on the occupancy of forest patches by Ovenbird and other Neotropical migrants, patch-scale processes such as an edge-related increase in nest predation or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) have received most of the attention (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove et al. 1986, Temple and Cary 1988). By contrast, the assessment of the potential im-

portance of processes acting at the landscape scale, such as the alteration of dispersal patterns by habitat fragmentation, is still largely based on correlational evidence (Lynch and Whigham 1984, Opdam et al. 1985, Askins and Philbrick 1987, Villard 1991).

Factors other than nest predation and brood parasitism may reduce the reproductive success of bird populations in fragmented habitats. In Missouri, Gibbs and Faaborg (1990) observed a significantly lower pairing success in Ovenbird populations of isolated forest patches (24% of all males paired) than in those of extensive forest tracts (75%). No trend was found in the Kentucky Warbler (*Oporornis formosus*), another area-sensitive species (Robbins 1979, Hayden et al. 1985, Robbins et al. 1989). Gibbs and Faaborg (1990) speculated that a higher predation rate on nesting female Ovenbirds might account for the surplus of males, since incubation is done entirely by the female in this ground-nesting species (Hann 1937). According to them, Kentucky Warbler nests in denser vegetation and, hence, incubating females are not as exposed to predators as in the Ovenbird. They also sug-

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gested that female Ovenbirds may prefer to breed in extensive forest tracts, where nesting success may be higher and food more abundant.

Wander (1985) observed the same trend as Gibbs and Faaborg (1990) in Ovenbird populations of New Jersey. She also found a lower pairing success in forest patches than in a control plot in an extensive forest. However, the difference, though significant, was of lower magnitude than that found by Gibbs and Faaborg (1990).

Because of the potential impact of a low pairing success on the persistence of the Ovenbird and other species in fragmented habitats, it is important to understand the factors responsible for this decreased success. For that purpose, we replicated the studies of Wander (1985) and Gibbs and Faaborg (1990) to examine the potential effects of local abundance and habitat fragmentation on pairing success. We tested the hypotheses that pairing success in Ovenbird populations: (1) increases with local population density; and (2) decreases with the degree of fragmentation of Ovenbird habitat in the surrounding landscape. These hypotheses emphasize processes occurring over two spatial scales. The first hypothesis implies that as the number of individuals increases, the probability of an even sex ratio (and higher pairing success) also increases by chance alone. We view it as a null hypothesis since it invokes a purely probabilistic phenomenon. The second hypothesis emphasizes landscape-scale processes that may vary according to habitat configuration. These hypotheses are not mutually exclusive, but their relative accuracy for explaining the variation in pairing success will be determined.

STUDY AREA AND METHODS

Ovenbirds were observed in a 25-ha plot in Gatineau Park, Québec (45°30'N, 75°50'W) in the 1990 and 1991 breeding seasons. Gatineau Park, hereafter referred to as the "extensive forest," covers more than 350 km² and is embedded in the extensive woodland of the Canadian Shield. This study plot was located 140 m away from a paved road with a narrow right-of-way, and 250 m away from a small field. The nearest significant gap in woodland was more than 1 km away. The location of the plot was chosen three weeks earlier than the arrival of the first males to avoid any bias.

In 1990, Ovenbird populations were studied in eight forest fragments (4.5–25.9 ha) surrounded by cultivated fields in an agricultural landscape immediately to the south of the extensive forest. Three of the eight sites were located in Québec, within 4 km of the edge of the extensive forest (45°28'N, 75°56'W), and the other five were located near Ottawa, Ontario, 20 km from the extensive forest (45°25'N, 76°10'W). In 1991, a single forest fragment (53.0 ha) was censused that was located 25 km east of the edge of the extensive forest, and approximately 55 km east of the forest fragments censused in 1990. This study site was found to have a fairly large Ovenbird population in earlier censuses (Villard 1991). Thus, we were interested in comparing pairing success in this larger fragment to that recorded in the sets of small ones censused in 1990.

The vegetation of all study sites was dominated by mature sugar maple (*Acer saccharum*), with some white ash (*Fraxinus americana*) and American basswood (*Tilia americana*). All stands had a closed canopy, but the density of the understory varied among fragments and within the 25-ha plot. None of the sites selected showed recent signs of cattle grazing, except along the edge of some of the forest fragments.

In the extensive forest, all Ovenbird territories overlapping the 25-ha plot were mapped using song playbacks (Falls 1981). Territory boundaries were drawn on a 25-m grid map. In 1991, two individuals were banded and individually marked on the breast with nontoxic paint to validate our mapping. These individuals remained within their mapped territory throughout the breeding season.

In the fragmented landscape, we recorded the location of each Ovenbird territory on maps drawn from 1:15,000 aerial photographs. In the extensive forest, the density of territorial males was measured as the number of territories located entirely inside the study plot plus one-half the number of territories overlapping the edge of the plot. In the forest patches, it was calculated as the total number of territorial males divided by the summed area of all patches, as in Wander (1985). Gibbs and Faaborg (1990) did not provide details on their calculation method.

Observations on pairing status were conducted after all territories were mapped, although evidence of pairing was found in a few instances during territory mapping. Pairing status was determined by monitoring the activities of focal territorial males using the same methodology as in Gibbs and Faaborg (1990), with the exception that the total duration of observation bouts varied among individuals. We finished our observations as soon as pairing status was ascertained with confidence (i.e. when a male was seen interacting with a female or carrying food, when a male or a female was seen with young, or when an active nest was found). A nonsinging individual tolerated by a male within a 5-m radius, or emitting series of "tsip" notes (Lein 1980), was considered to be its female mate. However, we rarely had to rely solely on this criterion in 1990, and paired males were either seen carrying food or with young in 1991. When

Fig. 1. Contour map of Ovenbird abundance (number of individuals·route^{-1}·year^{-1}) over its breeding range based on universal kriging of Breeding Bird Survey (BBS) data for the 1980–1989 period (courtesy of S. G. Heywood and B. A. Maurer). Quadrats (ca. 350 km on a side) centered on (Q) Québec-Ontario, (M) Missouri, and (N) New Jersey study areas. Contour lines may be erroneous above dotted line due to sparseness of surveys.

no evidence of pairing was found in the first observation bout, males were monitored for additional time so that the total observation time reached at least 90 min. In 1991, we used a dictaphone to measure track time instead of observation time. Track time is defined as the amount of time during which a bird is followed without losing visual or aural contact (Probst and Hayes 1987). Hence, track time is less sensitive than observation time to the variability in the visibility among and within study sites (Probst and Hayes 1987). In 1991, we monitored males until evidence of pairing was obtained, or until the total track time reached at least 90 min.

We compared our results to those of Wander (1985) and Gibbs and Faaborg (1990). Wander (1985) studied Ovenbird populations in a 20-ha study plot in an extensive forest (100 km²), and in 14 forest patches (1.7–37.2 ha). Gibbs and Faaborg (1990) conducted their study in five plots (18–32 ha) within large (>5 km²) tracts of woodland, and in six study plots (9–51 ha) within forest patches (9–140 ha). New Jersey and Missouri data used in this study were extracted from tables in Wander (1985) and Gibbs and Faaborg (1990), and used to compute new statistical tests. The location of each study area is shown on Figure 1, which depicts contour lines of Ovenbird abundance throughout its breeding range, based on Breeding Bird Survey (BBS) data (see Robbins et al. 1986) for the 1980–1989 period.

We calculated the mean abundance of the species in squares of approximately 350 km on a side that were centered on each study area. We had to use these relatively large squares in order to obtain a sufficiently large number of BBS routes around the Québec-Ontario study area.

We used G-tests (Sokal and Rohlf 1981) to compare pairing success between extensive and fragmented forests in each study and year. The relationship between territorial male density and pairing success was examined graphically by constructing a scatter plot and choosing the curve of best fit to illustrate the general trend. We used territorial male density instead of total population density, since the number of known females in the population increases with pairing success and this would have biased the relationship. We assumed that territorial male density is a reliable indicator of the potential density of breeding pairs in a site.

We then used general linear models (SAS 1990; PROC GLM) to quantify the relative contribution of woodland configuration (extensive vs. fragmented forests) and geographic location for explaining the variability in territorial-male density and pairing success. The GLM procedure was used instead of an analysis of variance because of unequal samples in one of the classification variables (geographic location). We computed two separate models, with pairing suc-

TABLE 1. Proportion of Ovenbird territorial males paired (pairing success) in extensive and fragmented forests in three widely separated portions of Ovenbird breeding range. Total number of territorial males shown in parentheses.

| | Percent pairing success | | |
Year	Extensive forest	Fragmented forest	G^a_{adj}
Québec-Ontario			
1990	82.4 (17)	58.6 (29)	2.788[+]
1991	76.5 (17)	58.3 (12)	0.908[ns]
New Jersey (Wander 1985)			
1982	81.3 (16)	41.7 (12)	4.479[*]
1983	86.7 (15)	58.1 (31)	3.960[*]
1984	86.7 (15)	53.3 (30)	5.115[*]
Missouri (Gibbs and Faaborg 1990)			
1988	75.0 (20)	23.5 (17)	9.744[**]

[a] G-test with Williams' correction on 2 × 2 contingency table (df = 1). +, $P < 0.10$; *, $P < 0.05$; **, $P < 0.005$; ns, $P > 0.25$.

cess (arcsine transformed; Sokal and Rohlf 1981) and territorial male density as respective dependent variables. We treated data sets from different years as independent observations, since the actual study sites visited varied between years (except between 1983 and 1984 in New Jersey study). The effect of geographic location was further examined using Scheffé's test (Sokal and Rohlf 1981, SAS Institute 1990) to determine the significance of pairwise differences in pairing success or territorial male density among the three locations. We also added an interaction term to determine whether the effect of woodland configuration on the dependent variables varied according to the geographic location.

RESULTS

Québec-Ontario study.—In 1991, mean track time for individuals found to be paired was 8.9 ± SD of 8.8 min ($n = 13$) in the extensive forest, and 16.4 ± 17.2 min ($n = 7$) in the fragmented forest. Mean track time for individuals deemed unpaired was 92.5 ± 2.9 min ($n = 4$) in the extensive forest, and 97.1 ± 3.6 min ($n = 5$) in the forest patches. Since eight individuals were found to be paired during territory mapping, we did not plot the curves of cumulative increase in percentage of males paired with track time (see Probst and Hayes 1987). However, the longest track times recorded to confirm that a male was paired were 28.0 and 44.5 min in the extensive and fragmented forests, respectively. Since these track times are substantially shorter than 90 min, we are confident that the values

we recorded for pairing success are valid, and that no substantial bias can be attributed to the use of observation time instead of track time in 1990.

Territorial males experienced a lower pairing success in the forest patches than in the extensive forest in both 1990 and 1991 (Table 1). However, the difference was not significant but suggestive ($P < 0.10$) in 1990 and was not significant (G-test, $P > 0.25$) in 1991. Pairing success was consistent between years in both the extensive forest and the forest fragments (G-tests, $P > 0.50$). Thus, the comparison of these results to those of Wander (1985) and Gibbs and Faaborg (1990) is warranted. The temporal consistency observed is especially noteworthy in the case of the forest fragments, considering the distance separating the 1990 and 1991 study sites.

New Jersey and Missouri studies.—Pairing success was lower in forest patches than in extensive forests both in the New Jersey and Missouri studies (Table 1). When compared to our data, these results indicate that the effect of habitat fragmentation is extreme in the Missouri study area, and relatively similar in Québec-Ontario and New Jersey study areas, although stronger in the latter. About 80% of territorial males were paired in study plots within extensive forests in the three widely separated study areas, while pairing success was more variable in fragmented forests. The fact that pairing success was lower than 100%, even in extensive forests, suggests a male-biased sex ratio in these populations.

Population density and pairing success.—We compiled density data from all three studies to examine whether pairing success increases with local population density. Although methods may vary between studies and variance estimates were unavailable, we wanted to determine the shape of the relationship between pairing success and the density of territorial males. Densities were higher in the extensive forests than in fragmented forests in all studies and years, as was the case for pairing success (Table 2). The density ratios are about 2:1 for extensive versus fragmented forests in Québec-Ontario and Missouri studies, while they range from 4:1 to 10:1 in the New Jersey study. In fragmented forests, density was highest in the Québec-Ontario study, while no clear difference was found between the New Jersey and Missouri studies.

The relationship between pairing success and the density of territorial males was best fit by

TABLE 2. Average density of Ovenbird territorial males (per 10 ha) in fragmented and extensive forests.

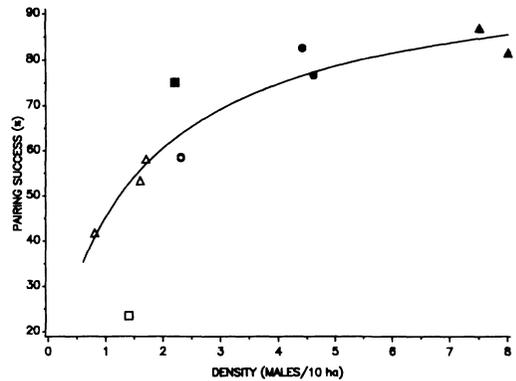| Year	Extensive forest	Fragmented forest
Québec-Ontario		
1990	4.4	2.3
1991	4.6	2.3
New Jersey (Wander 1985)		
1982	8.0	0.8
1983	7.5	1.7
1984	7.5	1.6
Missouri (Gibbs and Faaborg 1990)		
1988	2.2	1.4

Fig. 2. Density of territorial males per 10 ha and pairing success in different Ovenbird populations. Symbols represent data points from Missouri (squares), New Jersey (triangles), and Québec-Ontario (circles). Open symbols represent data from fragmented forests and closed symbols correspond to extensive forests. Open circle and second closed triangle from right each represent two superimposed data points.

a logit curve (Fig. 2), which indicates that pairing success rises at a decreasing rate with territorial male density. By including many years of data from the same study areas, we were guilty of pseudoreplication. However, only the points from the New Jersey fragmented forest show substantial variation among years. The tendency of the curve to level off at higher densities remains whether or not we use average values for Québec-Ontario and New Jersey data sets. Figure 2 shows that pairing success is higher in populations of extensive forests, even at similar densities of territorial males (compare Missouri extensive forest and Québec-Ontario fragmented forests). Also, the data points that depart the most from the logit curve are those from the Missouri study. Pairing success was substantially lower in the forest patches of the Missouri study than in the fragmented forests of the Québec-Ontario and New Jersey studies. The density of territorial males also was lower in the extensive forests of the Missouri study than in those of the New Jersey and Québec-Ontario studies. The peripheral location of the Missouri study area in the breeding range of the Ovenbird may be related to this departure from the general trend (see Fig. 1 and Discussion).

Our first hypothesis, thus, is accepted, since there is a monotonic relationship between pairing success and territorial male density. However, the effect of territorial male density on pairing success becomes very weak when density exceeds four males per 10 ha.

Pairing success and habitat fragmentation.—The degree of woodland fragmentation may be compared among the agricultural landscapes of the

Québec-Ontario, New Jersey, and Missouri study areas. Wander (1985) measured the relative isolation of her study patches as the distance to the nearest neighboring patch 10 ha or larger. Our 1990 study sites were closer to neighboring woodland than those of Wander (1985), with a mean distance of 0.35 ± 0.06 km $(n = 8)$, compared to 0.99 ± 1.07 km $(n = 14)$ in the New Jersey study. However, that difference is not significant $(t = 1.68, df = 20, \text{two-tailed } P > 0.10)$. When including our 1991 study site (0.05 km away from nearest patch > 10 ha), the difference approaches statistical significance $(t = 1.86, df = 21, P < 0.10)$. Gibbs and Faaborg (1990) measured patch isolation as the percentage of woodland within 5 km of their study plots. They obtained values ranging between 18 and 20%. Since our 1990 forest patches were spatially clustered and, thus, likely to give spatially autocorrelated values for this isolation variable, we calculated the percentage of woodland in circles of 5-km radius centered on each cluster of study sites. We obtained 38 and 40% woodland for the two clusters of study sites. Our 1991 study site was surrounded by only 15% woodland within a 5-km radius. The high values for 1990 study sites are due mainly to the proximity of each cluster to an extensive forest (Gatineau Park, and Carp Ridge forest, respectively).

Thus, our 1990 sites were located in agricul-

TABLE 3. Effect of geographic location and woodland configuration on Ovenbird (A) pairing success and (B) territorial male density as determined by general linear models.

Classification variables	F	P
Pairing success[a]		
Model	28.19	0.0004
Geographic location[b]	10.49	0.0110
Woodland configuration[c]	104.58	0.0001
Interaction term[d]	4.85	0.0557
Density of territorial males		
Model	133.01	0.0001
Geographic location	50.64	0.0002
Woodland configuration	208.54	0.0001
Interaction term	68.96	0.0001

[a] Arcsine transformed.
[b] Québec-Ontario, New Jersey, or Missouri.
[c] Extensive or fragmented forest.
[d] Interaction of geographic location and woodland configuration.

tural landscapes that had approximately twice as much forest cover as did the Missouri farmland surrounding Gibbs and Faaborg's (1990) forest patches. Our 1991 site, however, appears relatively isolated, using the same criterion, but it was relatively close (6.3 km) to the extensive forests of the Canadian Shield.

As mentioned earlier, pairing success does not differ significantly between fragmented forests of the Québec-Ontario and New Jersey studies, which suggests that the slightly greater isolation of New Jersey forest patches is insufficient to affect their accessibility. However, pairing success varied within the New Jersey study area. Six of Wander's (1985) study sites (1.7–26.7 ha) were clustered together, with no gaps exceeding 100 m. Pairing success was higher in this cluster of forest patches than in more isolated patches in each of the three years of her study, although a significant difference was found only in 1983 (G-test, $G_{adj} = 3.984$, df = 1, $P < 0.05$).

Effects of geographic location and woodland configuration.—Pairing success varied with both geographic location and woodland configuration, while the interaction term combining these two variables was nearly significant (Table 3). The model was very highly significant overall. Woodland configuration had a more significant effect on pairing success than geographic location. The effect of geographic location on pairing success was mainly due to the difference between the Missouri study and the two other studies (Scheffé's test, $P < 0.05$). This result, together with the near significance of the in-

teraction term, suggests that the effect of woodland configuration on pairing success was more severe in the Missouri study area.

Since territorial male density and pairing success are interrelated, we computed a second model with territorial male density as the dependent variable and the same classification variables as above. Again, the model was very highly significant (Table 3), but the interaction term much more pronounced than in the previous model, indicating that territorial male density varied with geographic location and woodland configuration, and that the combined effect of geographic location and woodland configuration varied among Québec-Ontario, New Jersey, and Missouri studies. Territorial male density varied much more between extensive and fragmented forests of Québec-Ontario and New Jersey studies than was the case in the Missouri study (Table 2). The results of these two models again point out the contrast of the Missouri study relative to the two other data sets.

Ovenbird regional abundance varies greatly with geographical location (Fig. 1). The Missouri study area is located at the periphery of the breeding range, in a zone of low abundance. By contrast, our study area is located in an area of fairly high abundance. We computed the mean abundance per route per year in quadrats of approximately 350 km on a side centered on each study area. Abundance was lowest around the Missouri study area (0.35 ± 1.40, n = 23) and highest in the vicinity of the Québec-Ontario study area (26.15 ± 9.86, n = 16). Ovenbird abundance was intermediate around the New Jersey study area (8.51 ± 11.44, n = 81).

DISCUSSION

As expected, pairing success in Ovenbird populations was lower in fragmented than in continuous tracts of habitat. Pairing success also increased with territorial-male density, although this trend gradually levelled off at high densities. A male-biased sex ratio was apparent in this and the other two studies examined, but pairing success was consistently lower in fragmented forests than in plots within extensive forests. A comparison among three studies showed that a reduction in territorial male density below approximately four territorial males per 10 ha was associated with a rapid reduction in pairing success. This reduction in density

and the factors causing it may, thus, have a critical impact on the productivity of Ovenbird populations.

Various hypotheses may be invoked to explain the increase in pairing success observed with territorial male density. Two lines of evidence indicate that the patterns we observed do not reflect a purely probabilistic phenomenon whereby larger populations achieve higher pairing success by chance alone. First, an identical proportion of territorial males were paired in the small populations of the eight small fragments surveyed in 1990 and in the larger population surveyed in 1991. Second, we would expect under this hypothesis that the sex ratio would be female-biased in some of the fragments and, thus, that most if not all males would be paired in these fragments, which was not the case. We propose four other hypotheses to explain the lower pairing success observed in fragmented forests: (1) female Ovenbirds actively select sites with high densities of territorial males (conspecific-attraction hypothesis), as suggested by Wander (1985); (2) females actively avoid breeding habitat bordering open habitats (habitat-selection hypothesis); (3) females prefer older males to yearlings (mate-selection hypothesis); (4) female mortality is particularly high during the breeding season in the sparse populations of fragmented forests (female-biased mortality rates), as proposed by Gibbs and Faaborg (1990). None of these hypotheses can be formally tested using the literature. However, we can discuss their relative merit based on the current knowledge of Ovenbird life history.

Conspecific attraction. —Smith and Peacock (1990) emphasized the potential influence of conspecific attraction on the metapopulation dynamics of animal species. They argued that animals may be more likely to leave a habitat patch if they detect conspecifics on nearby patches, and that they may be more likely to settle in an occupied patch of habitat than in a vacant one. Wander (1985) suggested that female Ovenbirds may use the density of territorial males as an index of habitat quality. Wander's (1985) hypothesis has not yet been tested on Ovenbird populations. The conspecific-attraction hypothesis implies that: (1) individuals (here, females) can search through several habitat fragments before selecting a territory; and that (2) these movements take place at a time when males frequently advertise their pres-

ence. In the Ovenbird, these movements would take place in the spring, upon the arrival of females on the breeding grounds. More information on the trajectory and timing of these movements, thus, is required to test this hypothesis.

Habitat selection.—Low pairing success in patch populations might be caused by a direct or indirect assessment of habitat quality by females, as suggested by Gibbs and Faaborg (1990). Probst and Hayes (1987) observed a consistently higher pairing success in Kirtland's Warblers (*Dendroica kirtlandii*) breeding in "suitable" habitats than in those inhabiting more marginal habitats. They classified habitats as suitable if they had been used by birds for at least three years. In the Ovenbird, indirect assessment of prey abundance through vegetation structural cues is supported by correlational evidence (Smith and Shugart 1987). If females actively selected habitat (and territory holders) in this fashion, this would imply that the fragmented forests in all three study areas, especially that in Missouri, were of marginal quality.

The habitat variables used by Smith and Shugart (1987) characterize the vertical structure of the vegetation. It is also conceivable that females may respond to horizontal characteristics of habitat, such as the distance to the nearest forest edge, which may influence prey abundance through its effect on litter moisture. Kroodsma (1984) found that Ovenbirds were one of the few species showing a significant pattern of edge avoidance. However, no studies have been conducted that compare the relative tendency of males and females of a given species to avoid habitat edges.

This hypothesis assumes that the movements of females are not constrained by woodland configuration, and that they may search over fairly large areas when selecting a territory. For the Collared Flycatcher (*Ficedula albicollis*), a Paleotropical migrant, Pärt (1991) compared reproductive success in pairs of yearling sisters and found that philopatric females laid more eggs and fledged more young per egg than their more dispersive sisters. Hence, this suggests that extensive exploratory movements by yearling females may not be advantageous. In his study area, birds could choose among patches differing in area and habitat characteristics. In the Ovenbird, older females tend to return to breed to the same area year after year (Hann 1937, Leck et al. 1988). Thus, the exploratory move-

ments implied by this sex-specific habitat-selection hypothesis are unlikely to be made by older females.

Mate selection.—The interaction of reproductive success, dispersal, and mate selection could also lead to the patterns observed in pairing success. In the American Redstart (*Setophaga ruticilla*), all unpaired territorial males found by Sherry and Holmes (1989) were yearlings. These yearlings were excluded by older males from certain mutually preferred habitats. However, it is not clear whether the breeding opportunities of these yearlings were strictly limited by older males, or by both age-specific dominance and intrinsic characteristics of yearlings making them less attractive to females. Assuming that females prefer older males, pairing success would be expected to decrease with the proportion of yearlings in the population.

In many species, birds that fail to fledge young tend to disperse more frequently or over longer distances to their next breeding site than successful breeders (Darley et al. 1977, Nolan 1978, Harvey et al. 1979, Shields 1984, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Pärt and Gustafsson 1989). If breeding pairs experience a higher probability of nesting failure in fragmented forests than in extensive woodland tracts, as seems to be the case (Wilcove 1985, Andrén 1992), this should lead to longer breeding dispersal movements in the former landscape type. Over several generations, this phenomenon could result in a gradual shift in age structure of the regional population of a fragmented forest favoring individuals breeding for the first time. This shift would be most extreme in forest patches where birds experience a consistently high incidence of nesting failure, and the greater extent of natal dispersal movements compared to movements of individuals having bred at least once would tend to reinforce this trend. Hence, this mechanism would be consistent with the observation of a lower pairing success in populations of fragmented forests, assuming that females prefer to mate with older males. This shift in age structure would also be expected to reflect the degree of habitat fragmentation. Despite the lack of a common isolation variable among this and the New Jersey and Missouri studies, both fragmentation and pairing success vary qualitatively as predicted by this hypothesis. No study has compared the age composition of breeding populations in fragmented versus extensive forests.

Female-biased mortality rates.—Because they spend the incubation period in relatively exposed ground nests, female Ovenbirds may be particularly susceptible to the intense predation recorded in fragmented forests (Gibbs and Faaborg 1990). Higher female mortality in fragmented forests would be consistent with the greater proportion of unpaired males observed in habitat fragments. No sex-specific mortality rates are available for this species in fragmented and extensive forests, preventing us from testing this hypothesis.

Implications for conservation.—Our results show that the reduction in Ovenbird pairing success associated with habitat fragmentation is not unique to the Missouri study, or to sites at the periphery of the breeding range of the species. Although less dramatic, similar tendencies were also found in more central portions of the breeding range. However, our analysis does suggest that forest fragmentation has a more severe effect in the Missouri study area than in Québec-Ontario or New Jersey study areas. Brown (1984) pointed out that many plant and animal species exhibit gradients in abundance within their geographic range, density being greatest near the center, and gradually decreasing toward the periphery. This pattern is seen in the Ovenbird. Since the Missouri study area is located at the periphery of Ovenbird's breeding range, the species might be particularly sensitive to the alteration of its habitat at the local or landscape scales, because environmental conditions are probably marginal in the first place (Brown 1984). Indeed, the effect of woodland configuration on territorial male density and pairing success was greater in Missouri than in New Jersey and Québec-Ontario.

The presence of unpaired territorial males has been reported in other primarily monogamous species, including Song Sparrow (*Melospiza melodia*; Smith and Arcese 1989), Black-throated Blue Warbler (*Dendroica caerulescens*; Holmes et al. 1992), Kentucky Warbler (Gibbs and Faaborg 1990), and American Redstart (Procter-Gray and Holmes 1981, Sherry and Holmes 1989). Smith and Arcese (1989) observed a density-related shift in the social status of yearling male Song Sparrows in an insular population. When territorial male density was high, they found a large number of nonterritorial individuals (floaters), most of which were yearling males. In years of low territorial male density, yearling males gained marginal territories, but most of

them remained unpaired. The presence of float-
ers also was demonstrated in the American Red-
start through removal experiments (Sherry and
Holmes 1989). Their study was conducted in an
extensive forest; hence, the presence of floaters
cannot be attributed to restricted juvenile dis-
persal.

Based on these patterns, we should observe
more floaters in the dense populations of ex-
tensive forests, and few or none in the sparser
populations of habitat fragments. The presence
of floaters in habitat fragments would suggest
that these populations are saturated, and that
low pairing success does not merely reflect
low-quality habitat. We have not observed any
floaters in our Ovenbird populations. Neither
Wander (1985) nor Gibbs and Faaborg (1990)
reported their presence. Floaters may have been
overlooked since the methodology used in all
three studies was based on the monitoring of
the activities of focal territorial males. Banding
and removal experiments would be required to
assess the existence and number of floaters in
Ovenbird populations.

Data from control plots in extensive forests
of Québec-Ontario, New Jersey, and Missouri
indicate that some males typically remain un-
paired, even in apparently "healthy" popula-
tions. However, the low pairing success record-
ed in fragmented forests in the three studies
considered here should substantially reduce the
productivity of these populations. Clearly, the
low pairing success of Ovenbirds in fragmented
forests does not have the same impact on the
status of the species as that observed in Kirt-
land's Warblers breeding in marginal habitats
(see Probst and Hayes 1987). The Ovenbird is
a widely distributed species that is still common
in its habitat. However, the situation reported
by Gibbs and Faaborg (1990), if consistent among
years, appears quite dramatic. The observation
of the same trend in the central portion of the
breeding range and the consistency of the pat-
tern in three widely separated locations should
be considered as early warning signs of major
population declines, since fragmented forests
are now found over a large portion of the breed-
ing range of the Ovenbird.

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