The Auk 118(2):380–388, 2001

EFFECTS OF HABITAT FRAGMENTATION ON PAIRING SUCCESS OF OVENBIRDS: IMPORTANCE OF MALE AGE AND FLOATER BEHAVIOR

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Abstract.—Between 1996 and 1998, we compared pairing success of territorial male Ovenbirds (*Seiurus aurocapillus*) in forest fragments created by forestry ($n = 3$) and agriculture ($n = 10$) to contiguous forest plots ($n = 3$) in the southern boreal mixedwood forest of central Saskatchewan. The percentage of Ovenbird males paired per site was lower in fragments created by agriculture (86 ± 3%) and forestry (87 ± 3%) than in contiguous forest (97 ± 3%). At the individual level, second-year males (82%) were less likely to be paired than after-second-year males (94%), whereas males closer to edges were less likely to be paired than those in forest interiors. Although pairing success differed among landscapes, those differences were smaller than reported in studies conducted in eastern North America. The high density of birds in our study area may have resulted in intense intraspecific competition, which could have prevented unpaired individuals from maintaining territories. Removal experiments in 1997 and 1998 demonstrated floaters occurred in contiguous forest, but rarely occurred in fragments created by agriculture. The presence of floaters in contiguous forest suggests the ratio of breeding to nonbreeding males in forest fragments and contiguous forest may be similar, but that the strategy (i.e. floater vs. territorial) used by unpaired birds may differ among landscapes. *Received 18 January 2000, accepted 16 September 2000.*

Within populations of passerine birds, many males are unsuccessful in acquiring a mate during the breeding season (Breitwisch 1989, Newton 1992). Many factors influence pairing success of males, including age, body condition, and territory quality (Breitwisch 1989, Muller et al. 1997). Pairing success is typically lowest in habitats with few individuals or where birds have reduced foraging or nesting success, or both (Probst and Hayes 1987, Holmes et al. 1996, Hunt 1996). Interactions between territory quality and male age also occur, because older males often force younger males into suboptimal breeding habitat where the probability of attracting a female is reduced (Ficken and Ficken 1966, Sherry and Holmes 1989, Holmes et al. 1996).

Previous studies have compared how age of males influences pairing success in different vegetation types (Krebs 1971, Holmes et al. 1996, Petit and Petit 1996). Less is known about whether habitat selection at landscape scales influences pairing success. For example, Ovenbirds (*Seiurus aurocapillus*) select mature deciduous or mixed forests with a closed canopy and relatively sparse understory (Smith and Shugart 1987, Van Horn and Donovan 1994). However, equally important to Ovenbirds are the relative amounts of edge and interior habitat, proportion of forest cover in an area, sizes of forest patches, and proximity to roads (Wenny et al. 1993, Burke and Nol 1998, Ortega and Capen 1999). In particular, pairing success of male Ovenbirds is lower near edges and in small forest fragments than in the interior of large blocks of forest (Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998).

Effects of forest fragmentation on pairing success of Ovenbirds have been studied primarily in landscapes fragmented by agriculture in eastern North America (Wander 1985, Gibbs and Faaborg 1990, Porneluzi et al. 1993). In general, those studies have found pairing success is lower in fragments isolated by agriculture than in contiguous forest. Comparisons of pairing success in contiguous forest and landscapes fragmented by forestry are rare, and results have been inconclusive (Hagan et al. 1996, Sabine et al. 1996). However, predation rates on songbird nests are often similar between contiguous forest and landscapes frag-

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mented by forestry, leading some researchers to conclude that fragmentation by forestry is less severe for birds than fragmentation by agriculture (Rudnicky and Hunter 1993, Andrén 1995, Bayne and Hobson 1997). However, few studies have compared effects of landscape fragmentation by different processes in the same geographic region. Thus, it is difficult to know whether birds react differently to landscapes fragmented by forestry or agriculture, or whether differences observed among studies are caused by regional differences.

Four hypotheses have been proposed to explain reduced pairing success of Ovenbird males in forest fragments relative to contiguous forest. The female-biased mortality hypothesis suggests that high predation on females by generalist predators (characteristic of fragmented landscapes) creates a surplus of males in forest fragments (Gibbs and Faaborg 1990). In the conspecific-attraction hypothesis, females actively select dense populations of territorial males, so males in small fragments or in areas with few conspecifics are less likely to be paired (Smith and Peacock 1990). The habitat-selection hypothesis argues that females avoid breeding near edges and in small or isolated forest fragments because of greater rates of nest predation, brood parasitism, or lower food availability (Van Horn et al. 1995, Burke and Nol 1998). Finally, the mate-selection hypothesis suggests females prefer older or larger males, or both, that tend to obtain better quality territories in larger forest fragments (Villard et al. 1993).

All of the above hypotheses assume unpaired males are territorial. However, unpaired Ovenbird males could also exist in contiguous forest, but might be ''floaters'' that do not defend a territory (Hensley and Cope 1951, Sherry and Holmes 1989, Newton 1992). In contrast, risks involved in floating among fragments in fragmented landscapes could be greater than in contiguous forest. Thus, male Ovenbirds might defend poor-quality territories in forest fragments where the probability of attracting a female is low, rather than increase mortality risk by being a floater. If that is the case, differences in pairing success of Ovenbirds between fragmented landscapes and contiguous forest may have more to do with differences in behavior and movement patterns of unpaired males than actual differences in the ratio of breeding to non-breeding males.

The objective of our study was to determine if forest fragmentation by forestry and agriculture influenced pairing success of Ovenbirds in the southern boreal forest. We tested whether pairing success of territorial males was lower in farm fragments and forestry fragments relative to contiguous forest and whether that was influenced by habitat selection (i.e. landscape features) or was more likely to be influenced by mate selection (i.e. age or body condition). To determine if conspecific attraction influenced pairing success, we used published data to make regional comparisons of pairing success between areas with different densities of males. Finally, we also conducted a series of removal experiments to establish whether unpaired males in contiguous forest were more likely to be floaters than in the fragmented agricultural landscape.

METHODS

Our study was conducted during May and June, 1996 through 1998, in and around the Prince Albert Model Forest (hereafter PAMF) in north central Saskatchewan (53°50′N, 105°50′W). PAMF is located in the mixed-wood section of the southern boreal forest (Bouman et al. 1996). Sites were located in mature (60+ years) to old (100+ years) aspen or mixed-wood forest, where trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) dominated the overstory. Other less-common tree species included black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and balsam poplar (*Populus balsamifera*). The shrub layer was variable in density and composition but included beaked hazelnut (*Corylus cornuta*), green alder (*Alnus crispa*), rose (*Rosa* spp.), red osier dogwood (*Cornus stolonifera*), and saskatoon (*Amelanchier alnifolia*).

Three distinct landscape types occur in our study area: (1) 387,500 ha of protected contiguous forest in Prince Albert National Park (hereafter contiguous forest); (2) 84,000 ha of commercial forest of which approximately 25% has been harvested since 1969 (hereafter *forestry fragments*); and (3) 135,000 ha of forest and agricultural land in the rural municipality of Paddockwood (hereafter *farm fragments*), of which 70% is grain fields, hay fields, or pasture and 23% is farm fragments (Bayne and Hobson 1997).

Pairing success of territorial males.—In each landscape, we established a series of grids marked with flagging tape at 50 m intervals. In the contiguous forest, we established three 12.25 ha grids (two in 1997 and one in 1998). Each grid was at least 100 m from any trail, road or waterbody. In forestry fragments

TABLE 1. The ratio of paired to unpaired male Ovenbirds observed each year at each site.

Site	Area (ha)	% forest cover[a]	1996	1997	1998
Farm fragments					
Bossemaier	5	25	0:1	—	1:1
Cabin	5	64	—	—	2:1
Triangle 1	5	18	—	2:1	—
Connolly	7	26	2:0	2:1	—
Hulit	10	63	—	—	3:1
Dinius	11	21	—	3:0	—
Dump	12	44	—	7:0	—
Dean	15	30	—	8:0	8:1
Bader	19	45	6:3	10:1	9:2
McConnell[b]	42	22	—	—	7:1
Forestry fragments					
Clarine Lake[b]	25	62	—	—	10:2
Snowfield[b]	25	50	—	11:2	—
Bear[b]	35	49	—	11:1	—
Contiguous forest					
Namekus Lake[b]	—	100	—	—	11:0
Mud Creek[b]	—	100	—	12:1	—
Powerline[b]	—	100	—	14:0	—

[a] Percentage of forested land within 1 km radius of each site.

[b] Birds were surveyed in a 12.25 ha portion.

surrounded by clear-cuts created since 1990 or permanent roads, we established three 12.25 ha grids (two in 1997 and one in 1998). Each grid bordered two edges but did not cover the entire fragment. Ten grids were established in the agricultural landscape. All farm fragments were completely isolated by agricultural fields or roads. Grids in farm fragments (5 to 42 ha) covered the entire fragment (Table 1), except for the 42 ha farm fragment where we only surveyed a 12.25 ha portion. All contiguous forest and fragments created by forestry were surveyed in one year. Six of the farm fragments were surveyed in only one year, whereas the other four were surveyed for at least two years (Table 1).

On each grid, all males were captured using song playback to draw birds into mist-nets. Once captured, all birds received a U.S. Fish and Wildlife Service aluminum band and three colored-plastic leg bands to form a unique band combination. Most birds were captured within two weeks of spring migration. Upon capture, we measured unflattened right wing chord (millimeters) and mass (grams), and plucked the third right rectrix as a means of aging birds (see below). Each bird was followed and their territory mapped using a combination of spot mapping and the playback technique of Villard et al. (1993). Each bird was followed for a cumulative period of 90 min or until evidence of pairing was observed. Birds were followed for a maximum of 30 min per day. Evidence of pairing included: (1) male seen in vicinity of female; (2) male carrying food; (3) male or female seen with young; or (4) an active nest was found within a territory. As Ovenbirds are monomorphic, a nonsinging individual tolerated by a male within a 5 m radius or emitting a series of ''*tsip*'' notes was considered its female mate (Lein 1980).

Age was determined using the wear pattern of the third rectrix. We classified each individual as either a second-year bird breeding for the first time (SY) or as an after-second-year bird (ASY), on the basis of the technique of Donovan and Stanley (1995). Individuals with a rectrix tip angle of ≤84 were classified as SY, whereas all birds with a feather tip angles greater than that were classed as ASY. One person who had no knowledge of where feathers were collected measured all feathers. To maximize precision, all feathers were measured in the laboratory by scanning each feather into a computer and expanding the image 700×. Images were printed and the angle of the feather tip measured using grid paper and a protractor.

Removal experiments.—To determine if colonization of territories by floaters was more likely to occur in contiguous forest than in farm fragments, removal experiments were conducted in one farm fragment and one contiguous forest site in both 1997 and 1998. Permanent grids were established at each removal site, and for four to five days before removal birds were surveyed on each grid using playback to plot territory locations. Evidence of pairing success was determined at that time. Before removal, males in territories adjacent to the removal zone were color banded. This ensured colonization by floaters was by new individuals and not by resident individuals increasing their territory size into the removal area (Newton 1992).

To avoid encountering migrant Ovenbirds, removals took place when females were incubating nests (12 June in farm fragments for both years and 15 June in 1997 and 13 June in 1998 for the contiguous forest plots). For two weeks following removal, we visited each site every day for the first three days and every second or third day after that to determine when or if floaters colonized areas where males were removed. A floater was defined as an unbanded bird that was observed singing in a removal territory. At days 12 through 14, we conducted comprehensive territory mapping to determine which territories had been filled.

Statistical analysis.—To determine if the pairing success of male Ovenbirds differed among landscapes, we used weighted least squares (WLS) ANOVA (Neter et al. 1985). In that analysis, the dependent variable was the percentage of male Ovenbirds paired per site, whereas the independent variable was landscape. The weighting variable was number of individuals recorded per site. We used a WLS approach because variance in percentage of male Ov-

TABLE 2. Density estimates (males per 10 ha) and percentage of males paired in contiguous forest and forest fragments across North America. Numbers in parentheses are the number of birds in each treatment for which pairing success was determined. Estimates of pairing success are the proportion of individuals paired within a particular study (i.e. sites within landscapes in each study were pooled).

State/province	Fragmented by	Density in forest	Density in fragment	% paired in forest	% paired in fragment	Reference
New Jersey	Agriculture	7.6	1.4	85 (46)	53 (73)	Wander 1985
Missouri	Agriculture	2.2	1.4	75 (20)	24 (17)	Gibbs and Faaborg 1990
Pennsylvania	Agriculture	6.9	3.0	67 (27)	47 (17)	Porneluzi et al. 1990
Ontario	Agriculture	4.5	2.3	82 (46)	63 (38)	Villard et al. 1993
Saskatchewan	Agriculture	8.7	5.2	97 (38)	84 (87)	This paper
New Brunswick	Forestry	1.9	1.1	91 (23)	82 (22)	Sabine et al. 1996
Maine	Forestry	6.1	8.4	80 (40)	52 (61)	Hagan et al. 1996
Saskatchewan	Forestry	8.7	7.5	97 (38)	86 (37)	This paper

enbirds paired was inherently higher in small fragments, simply because fewer males were present in those sites (i.e. estimates of pairing success were less precise in small fragments than in larger fragments). Each data point was weighted by the term:

$$w = 1/X \quad (1)$$

where w_i was the weighting term applied to each data point and X was the number of individuals per site (Neter et al. 1985). By weighting each data point by number of individuals per site, we reduced the importance of small farm fragments where only one or two individuals were present and placed more emphasis on the larger sites where more individuals were recorded (Neter et al. 1985). Logistic regression was also used to determine if landscape effects were influenced by individual characteristics such as age (SY vs. ASY), distance from edge (edge), body condition, edge × landscape, and age × body condition. Body condition was the residuals from a linear regression model that used wing length, time of day, and Julian date to predict mass (Bayne 2000). To create the most parsimonious model that explained the greatest amount of variation in the data, we employed a step-down approach in creating the most parsimonious logistic regression model (Lebreton et al. 1992). First, we looked at all possible combinations of interactions while controlling for main effects. On the basis of the change in the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 1998), we then decided whether to retain each interaction in the model. We then examined all possible combinations of main effects. Once the most parsimonious model was obtained (had the lowest AICc), we double-checked the importance of the interactions that were previously removed, by reentering each interaction into the model. If two or more models had similar AICc values (<2), we chose the most parsimonious model with the fewest parameters.

To determine if pairing success of Ovenbirds was dependent on population density, we conducted an analysis using the results of published studies. To be included in that analysis, we required a study to report pairing success and Ovenbird density for fragments surrounded by agricultural land or fragments surrounded by clear-cuts versus contiguous forest. Using logistic regression, we determined if the proportion of paired male Ovenbirds was influenced by landscape, density of territorial males (males per 10 ha), or the interaction between landscape and density. Again, model selection was based on AICc values.

RESULTS

Pairing success of territorial males.—Pairing success was determined for 162 males (Table 1). Seven paired males that could not be captured were assumed to be SY birds, and were given average wing and mass values for pairing success analyses. The percentage of males paired per site (weighted least squares means ±1 SE) was significantly lower in farm (86 ± 3) and forestry fragments (87 ± 3) than in contiguous forest (97 ± 3: $F = 3.7$, df = 2 and 21, $P = 0.05$). The logistic regression model with the lowest AICc value included age ($\chi^2 = 4.2$, df = 1, $P = 0.02$) and the distance a male's territory was from an edge ($\chi^2 = 8.2$, df = 1, $P = 0.004$). SY birds had a lower probability (82% of 83 males) of being paired than ASY birds (94% of 79 males). The territories of unpaired birds had a shorter median distance from edge (55 m; range = 20 to 140 m) than paired birds (80 m; range 20 to 500 m). The edge effect occurred equally across landscapes, as the interaction between edge and landscape was not significant ($\chi^2 = 1.5$, df = 1, $P = 0.48$).

Comparisons with other studies.—For all studies combined (Table 2), the logistic regression

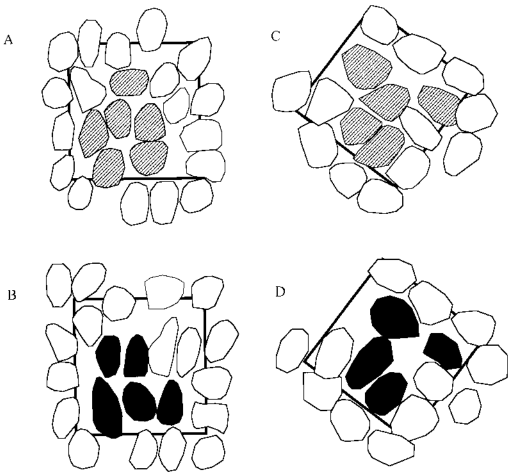

FIG. 1. Territory locations of male Ovenbirds on removal grids in contiguous forest: (A) prior to removal of six males in 1997; (B) two weeks after removal in 1997 with colonization by five floaters; (C) prior to removal of five males in 1998; and (D) two weeks after removal in 1998 with colonization by four males. Individuals with: (1) hatched pattern were removed; (2) solid white pattern were color banded and remained on the site; and (3) solid black were floaters that recolonized vacant territories. The square represents the boundary of a 9 ha removal grid which was bordered on all sides by forest of similar composition. Scale is approximately 1 to 6,000.

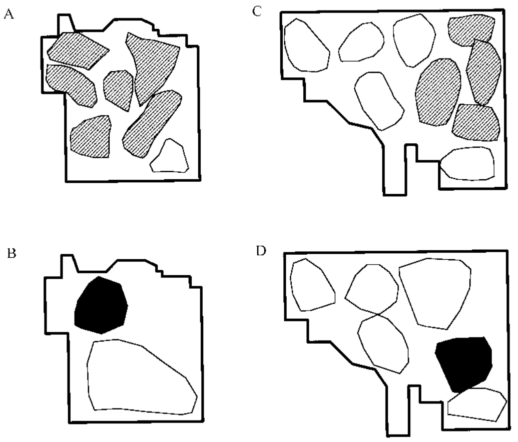

FIG. 2. Territory locations of male Ovenbirds on removal grids in the agricultural landscape: (A) prior to removal of six males in 1997; (B) two weeks after removal in 1997 with colonization by one floater; (C) prior to removal of four males in 1998; and (D) two weeks after removal in 1998 with colonization by one floater. Individuals with: (1) hatched pattern were removed; (2) solid white pattern were color banded and remained on the site; and (3) solid black were floaters that recolonized vacant territories. The boundaries of these grids were adjacent to grain fields. The 1997 grid was 11 ha and the 1998 grid was 15 ha. Scale is approximately 1 to 6,000.

model with the lowest AICc included landscape and interaction between landscape and density. Farm fragments and forestry fragments had a lower proportion of paired males (63% of 246 males and 67% of 122 males, respectively) than contiguous forest (82% of 236 males: $\chi^2 = 21.3$, df $= 2$, $P = 0.001$). The proportion of paired males was positively correlated with density in farm fragments ($\chi^2 = 18.2$, df $= 1$, $r = 0.22$, $P = 0.001$), negatively correlated with density in forestry fragments ($\chi^2 = 3.8$, df $= 1$, $r = -0.11$, $P = 0.05$), and not influenced by density in contiguous forest ($\chi^2 = 0.02$, df $= 1$, $P = 0.89$).

Removal experiments.—In 1997, we removed six males from the contiguous forest grid (Fig. 1A). Within one day, two new males were observed on the plot. On day two, a third individual was observed. By day 10, five new males were present and remained until the end of the experiment (Fig. 1B). Of the five floaters that settled, four were seen with females. Two territorial males, on the plot before removals occurred, shifted their territories (Fig. 1B). During 1998 in the contiguous forest, we removed five males (Fig. 1C). Within one day, two males had colonized the empty territories. Another two males were observed on day 10 (Fig. 1D). All floater males in 1998 were observed with females by the end of the experiment.

In 1997, we removed six of seven resident males from an 11 ha farm fragment (Fig. 2A). On day nine, one new male established a territory at the north end of the plot (Fig. 2B). The individual that was present before removal was observed moving throughout the farm fragment. In 1998, we removed four males from a possible nine in a 15 ha farm fragment (Fig. 2C). Of the territory holders removed, three were paired and one was unpaired. The only new male observed in the 1998 farm fragment gained a territory on day six and held that territory until the end of the experiment (Fig. 2D). Floaters in the farm fragments were not observed with females, although the amount of observation time was less than our 90 min cutoff. Only three floaters could be captured; two were SY males.

DISCUSSION

Landscape factors such as fragment size, distance of territory from edge, and the amount of local forest cover surrounding fragments influence pairing success of territorial Ovenbirds (Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). In this study, males with territories farther from edges had a greater probability of attracting a mate. That apparent edge avoidance by females is similar to Van Horn et al. (1995), who found in an agricultural landscape in Missouri that 22% of males within 300 m of an edge were paired, whereas 76% of males with territories >300 m from an edge were paired. Similarly, the proportion of paired Ovenbirds was greater in patches with more core area in southern Ontario, an effect attributed to the reluctance of females to nest near edges (Burke and Nol 1998).

Avoidance of edges by female Ovenbirds has been attributed to increased nest predation and brood parasitism near edges (Van Horn et al. 1995, Burke and Nol 1998). Nest survival of Ovenbirds and other forest birds in our study area was lower in small farm fragments relative to contiguous forest (Bayne 2000, Hobson and Bayne 2000). A study using artificial nests in our study area, found ground nests at edges of farm fragments were 25% more likely to be destroyed than nests at edges of forestry fragments or in contiguous forest (Bayne and Hobson 1997). Those results imply the type of edge and the landscape in which it occurs may be important factors influencing nesting success (Bayne and Hobson 1997, Donovan et al. 1997). However, the interacting effect of landscape and edge did not affect pairing success, suggesting that type of edge had little effect on pairing success.

Young male Ovenbirds had a lower probability of attracting females than older males. Numerous studies have shown older birds to have greater pairing success than younger birds (Sæther 1990). Although many factors limit breeding success of younger males, territorial behavior of older males may force younger males into suboptimal habitats where they are less likely to attract mates (Van Horne 1983, Breitwisch 1989, Sherry and Holmes 1989). In a companion study (Bayne 2000), we found the proportion of SY males was higher in farm fragments than in forestry fragments or contiguous forest. A skewed age-ratio among landscapes suggests older males in forested habitats may preempt younger males and force them to breed in suboptimal habitats in farm fragments. At a regional scale, the proportion of SY Black-throated Blue Warblers (*Dendroica caerulescens*) was greatest at the edge of the range of that species (Graves 1997). Graves (1997) argued peripheral populations exist in sink habitats and are filled by SY birds that are forced to leave source habitats at the center of the range because of competition from older birds.

Another factor influencing pairing success in Ovenbirds is adult survival. That Ovenbirds are monogamous, not all males are paired, and unpaired females are rarely observed (Hensley and Cope 1951, Villard et al. 1993, Marra and Holmes 1997 but see Sæther and Fonstad 1981), suggests female survival is lower than male survival. Gibbs and Faaborg (1990) argued the difference in pairing success of Ovenbirds between fragments and contiguous forest was likely caused by greater female mortality in fragments. However, survival of females need not be different among landscapes for differences to exist in pairing success among landscapes. Female Ovenbirds may preferentially choose territories in contiguous forest and use lower quality fragments only when territories in contiguous forest are filled. If females preferentially select contiguous forest, then small differences in survival between males and females at a regional level would also cause a greater male sex bias in fragments, because a smaller proportion of the females would be forced to settle in fragments (Bayne 2000).

Density of male Ovenbirds in different regions of North America did not influence pairing success in contiguous forest. Thus, females do not avoid areas with low densities of males per se, suggesting conspecific attraction has little effect on pairing success. In fact, pairing success was negatively correlated with population density in harvested landscapes. This result was caused by low rates of pairing success in high-density Ovenbird populations in Maine, where immediately after clear-cutting, Ovenbirds from harvested areas forced themselves into remaining forest (Hagan et al. 1996). Hagan et al. (1996) argued increased intraspecific competition caused by high densities made it difficult for male Ovenbirds to maintain pair bonds in that habitat. In contrast, the forestry fragments examined in this study and those of Sabine et al. (1996) existed in a matrix of regenerating forest stands cut within the last decade. High rates of pairing success in stands surrounded by regenerating forest relative to those found immediately after clear-cutting suggests normal conditions within intact forestry fragments may become reestablished relatively quickly after disturbance to the surrounding forest, although they still may not reach those observed in contiguous forest. In contrast, regional density of Ovenbirds was positively correlated with pairing success in agricultural landscapes. Why density of male Ovenbirds influences pairing success in agricultural landscapes at a regional scale, but not in contiguous forest, is unclear. Regardless, those data indicate that in regions where the density of male Ovenbirds is lower, effect of fragmentation by agriculture on pairing success is most severe (Villard et al. 1993).

Removal experiments demonstrated some unpaired Ovenbirds were floaters. Floaters are typically late-arriving males that fail to acquire territories and, as a result, spend their time wandering among territory holders (Newton 1992). Assuming floaters are looking for a territory vacancy, those data suggest habitat in contiguous forest is saturated and that preemptive behavior limits number of breeding males that obtain territories (Newton 1992). However, Marra and Holmes (1997) argued removal experiments do not necessarily demonstrate habitat saturation. When male and female Black-throated Blue Warblers from the same territory were removed, colonization by other males was rare, but when males were removed and females were present, most territories were colonized by a new male or an adjacent territory holder (Marra and Holmes 1997). Thus, Marra and Holmes (1997) argued removal experiments test for the relative availability of females rather than the availability of habitat per se.

The notion that fragments have a lower proportion of paired males relative to contiguous forest has been based exclusively on observation of males that are territorial (Villard et al. 1993). However, unpaired floaters were more likely to fill territory vacancies in contiguous forest than in farm fragments, suggesting the ratio of paired to unpaired males may be similar in contiguous forest and farm fragments, but the strategies employed by unpaired males among landscapes are different. Potentially, floating in an open landscape matrix with fields or clear-cuts may increase predation risk relative to contiguous forest (Wesolowski 1981). Alternatively, the greater density of males in contiguous forest plots (Bayne 2000) may create more intraspecific competition relative to farm fragments (Newton 1992). With increased competition, males in contiguous forest may be more prone to float relative to males in forest fragments. In fragments, where the density of males is lower (Bayne 2000), Ovenbird males may be better able to maintain territories, although they may not attract a mate (Smith and Arcese 1989, Newton 1992). However, whether floaters are an important component of Ovenbird populations in other areas of their range is unknown (but see Hensley and Cope 1951). Density of Ovenbirds in the boreal forest of central Saskatchewan is two to five times higher than in most areas of North America. Thus, existence of floaters in our study area may be a consequence of the extremely high density and presumably high productivity of Ovenbirds in that region.

Like most removal experiments, the origin of our floaters was not known (Newton 1992, Marra and Holmes 1997). Banding nearby territory holders demonstrated that replacement individuals were not residents expanding their territory. However, whether the floaters came from a true nonterritorial population or were territorial individuals that had already suffered breeding failure and were attempting to locate a new territory is unknown. During the study, 12 banded males that demonstrated territorial behavior disappeared before the end of the breeding season, suggesting some of the Ovenbirds observed as floaters may have dispersed into the removal area from a previously held territory. Porneluzi and Faaborg (1999) found that paired Ovenbird males that failed to raise young almost never returned to the territory they held in a previous year, which they attributed to increased dispersal of failed breeders between breeding seasons. However, most direct evidence for within-season breeding dispersal by passerines following breeding failure indicates females are more likely to move than territorial males (Jackson et al. 1989).

The results of our study and those of others suggest that pairing success of Ovenbirds can be influenced by habitat fragmentation. Our data suggest that differential pairing success among landscapes is the result of female mate selection and female selection for habitats where nesting success is high. Survival differences among male and female Ovenbirds undoubtedly exist, but whether those are landscape specific remains unclear. Density of conspecifics does not seem to influence pairing success of territorial Ovenbirds, but the presence of floaters could result from the extremely high density of birds in our study area. Removal experiments in other areas of the Ovenbirds' range would help address whether the existence of floaters is due to limited habitat, whether the number of females in the population regulates the ratio of territorial to floater males, and if unpaired males use different strategies in different landscapes.

Acknowledgments

E. Cumming, S. Van Wilgenburg, B. Chruchz, S. Wyshynski, D. Jones, C. Oliarnyk, J. Ball, D. Mazerolle, T. McGregor, and H. Carlisle assisted in the field. R. Madro measured feather angles. Funding was provided by the Canadian Wildlife Service, Prince Albert National Park, and Prince Albert Model Forest (Project 211). Personal support to E.M.B. was provided by a Natural Sciences and Engineering Research Council of Canada scholarship and a graduate fellowship from the University of Saskatchewan. Special thanks from E.M.B. to the Canadian Wildlife Service for providing logistical support and office space. Thanks also to the landowners that allowed us to conduct this work on their land. The comments of D. Capen, J. Faaborg, B. Loiselle, and M.-A. Villard improved previous drafts of the manuscript. All Ovenbirds were captured under permits from Environment Canada and the University of Saskatchewan Animal Care Committee.

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Associate Editor: B. Loiselle