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APPARENT SURVIVAL OF MALE OVENBIRDS IN FRAGMENTED AND FORESTED BOREAL LANDSCAPES

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Abstract. From 1996 to 1999, apparent annual survival of male Ovenbirds (*Seiurus aurocapillus*) was compared in forest fragments created by forestry ($n = 3$) and agriculture ($n = 14$) to plots in continuous boreal forest of central Saskatchewan ($n = 3$). For 398 male Ovenbirds, Cormack-Jolly-Seber models indicated that apparent annual survival was lower (34%) in small forest fragments (<15 ha) in the agricultural landscape than in forestry fragments (56%) or continuous forest (62%). Our results suggested that lower nesting and pairing success in small forest fragments caused individuals to permanently disperse in search of new territories, rather than fragmentation increasing mortality. Regardless of the mechanism, increased turnover of adult males altered the age structure of the population in small forest fragments, as more males were first-time breeders in fragments in the agricultural landscape (59%) than in forestry fragments (47%) or continuous forest (45%). Males recruited into fragments in the agricultural landscape were more likely (90%) to be first-time breeders than in forestry fragments (74%) or continuous forest (64%). Our results suggest that adult dispersal differs with the amount and type of fragmentation and may play an important role in the population dynamics of boreal forest songbird populations.

Key words: adult survival; age structure; boreal forest; dispersal; fragmentation; nest success; Ovenbird; Saskatchewan, Canada; Seiurus aurocapillus.

INTRODUCTION

Theoretical and empirical research into the effects of forest fragmentation on bird populations has focused on the consequences of differential reproductive success between habitats (Donovan et al. 1995*a, b*, Hoover et al. 1995, Robinson et al. 1995, Trine 1998). Less is known about the effects of habitat fragmentation on adult survival or dispersal (Porneluzi and Faaborg 1999). However, many species of forest songbirds show a high degree of breeding-site fidelity (Greenwood and Harvey 1982, Holmes and Sherry 1992). Reproductive success in a previous year is often a good predictor of return rate, with birds unsuccessful at breeding being less likely to return to sites than birds that raised young (Roth and Johnson 1993, Murphy 1996, Haas 1998). Reproductive success of many forest songbirds is higher in large tracts of forest than in smaller, more fragmented forest patches (Wilcove 1985, Donovan et al. 1995*b*, Robinson et al. 1995), suggesting that return rates to fragmented areas should be lower than in continuous forest.

Lower breeding success in fragmented landscapes relative to continuous forest can be caused by several factors, but often results from increased nest predation (Wilcove 1985, Paton 1994, Bayne and Hobson 1997). Higher nest predation in forest fragments is typically caused by increased numbers of nest predators and changes in the composition of predator communities relative to continuous forest (Morrell and Yahner 1995, Oehler and Litvaitis 1996, Bayne and Hobson 1997, Kurki et al. 1998). If nest predators common to agricultural landscapes also kill adult songbirds, then adult songbirds may suffer higher rates of mortality in small fragments relative to continuous forest. Regardless of the mechanism (i.e., direct mortality or increased dispersal), understanding how habitat fragmentation influences our estimation of adult survival is crucial, because differential patterns of apparent survival among habitats can have a strong effect on the way we interpret landscape-level population models.

Previous demographic comparisons of passerine populations have shown that poor-quality habitats are maintained through immigration of young birds breeding for the first time (Holmes et al. 1996, Petit and Petit 1996). Young birds are assumed to colonize poor-quality habitat because they are preempted from breeding in high-quality habitat by older birds (Sherry and Holmes 1989, Pulliam 1996). However, most studies examining differences in the age structure of bird populations have compared adjacent vegetation types. Whether preemptive territory behavior functions at a landscape scale and leads to differences in age structure of populations in fragmented and continuous forest remains poorly understood (but see Graves 1997, Huhta et al. 1998).

Many landscape-level factors influence habitat qual-

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PLATE 1. Male Ovenbird banded in Prince Albert National Park, Saskatchewan, Canada. Photograph by Dan Mazerolle.

ity for forest songbirds. Forest interior passerines are typically less abundant in small, isolated forest patches (reviewed by Walters 1998). However, the majority of landscape-level studies on bird communities have been conducted in highly fragmented agricultural landscapes. Less is known about the way birds react to landscapes fragmented by forestry (Andrén 1995). Rates of predation on natural and artificial songbird nests at edges of clearcuts are often similar to those in the interior of forest patches, suggesting that fragmentation effects caused by forestry may be less severe than fragmentation by agriculture (Hanski et al. 1996, King et al. 1996, Bayne and Hobson 1997). However, few studies have compared the effects of landscape fragmentation by different anthropogenic processes in the same geographic region, so previous differences among studies could be the result of regional effects rather than differences between landscapes fragmented by forestry and agriculture per se.

The objective of our study was to compare aspects of Ovenbird (*Seiurus aurocapillus*; see Plate 1) demography among landscapes fragmented by agriculture and forestry to sites in continuous boreal mixed-wood forest of central Saskatchewan. We hypothesized that reproductive success would be lower in landscapes fragmented by agriculture than in landscapes fragmented by forestry or in continuous forest. We expected that males in the fragmented agricultural landscape would have lower apparent survival than in continuous forest because of permanent dispersal from sites where reproductive success was low. Low apparent survival of adults in forest fragments in the agricultural landscape was expected to cause a shift in the age structure of Ovenbird populations, with a greater percentage of younger individuals occurring in forest fragments than in continuous forest.

METHODS

Study area

Our study was conducted in the southern boreal mixed-wood forest of central Saskatchewan (Canada) from 1996 to 1999 (Fig. 1). Sites in continuous forest were located in Prince Albert National Park (PANP), a 387 500-ha protected area surrounded by agricultural land and commercial forest (53°57′ N, 106°22′ W). Sites in the agricultural landscape were in the rural municipality of Paddockwood (53°31′ N, 105°34′ W), a 135 000-ha area of privately owned land, of which 70% is used for agriculture and 25% is forest fragments. Sampling in the harvested landscape was conducted in the eastern block of Weyerhaeuser Canada's Forest Management Area (FMA) near Candle Lake, Saskatchewan (53°50′ N, 105°18′ W). Clear-cutting had removed ~25% of the mature forest in the harvested landscape since 1969. Forests in all landscapes were dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*), with some black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The shrub layer was variable in density and composition, with beaked hazelnut (*Corylus cornuta*), red osier dogwood (*Cornus stolonifera*), green alder (*Alnus crispa*), and white spruce saplings being the most common shrub species.

Sites were selected from 1:12 500 aerial photo and forest inventory maps, based on tree composition, age, lack of disturbance (e.g., cattle grazing or selective timber harvest), and area. Sites in all landscapes were dominated by aspen, with some sites containing ~25% white spruce. All stands had naturally regenerated following fire and were 70–110 yr old. Farm fragments were completely isolated from other fragments by a field or pasture and ranged from 5 to 42 ha (Table 1). The distance among sampled patches was ≥1 km. Each forestry fragment was isolated by a major-haul road on one side, a clearcut <5 yr old (at the start of the project) on the adjacent corner, and regenerating clearcuts <20 yr old on the remaining two sides. Continuous forest sites were chosen from forest inventory maps for PANP and were located in upland forests similar in age and composition to those surveyed in the fragmented landscapes.

Capture methodology

In forest stands within each landscape, we created a series of grids using flagging to identify 50 × 50 m cells. In the continuous forest, two 25-ha grids were surveyed from 1996 through 1999, with an additional 12.25-ha grid added in 1998. Each grid was ≥100 m from any hiking trail, road, or body of water. In frag-

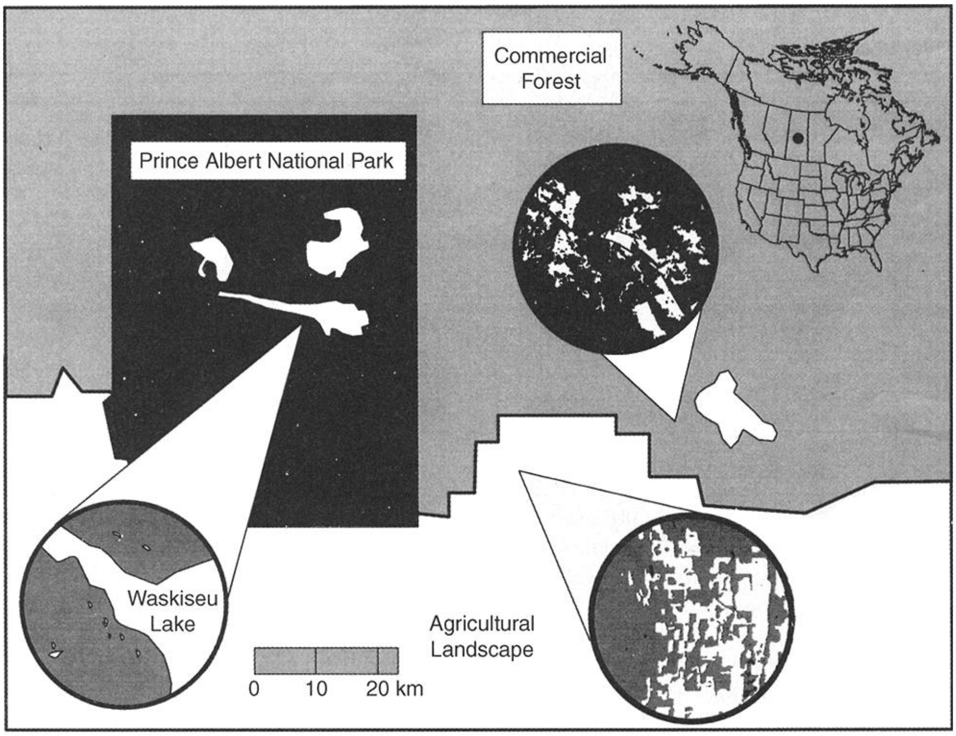

FIG. 1. Location of the study area in Saskatchewan, Canada. The dark area within circles represents the amount of forested land within a 5-km radius of one site in each landscape. Light areas represent bodies of water in the continuous forest, clearcuts made since 1980 in the harvested landscape, and hay fields or cropland in the agricultural landscape.

ments surrounded by clearcuts, a 32-ha and a 20-ha grid were surveyed every year, with an additional 12.25-ha grid added in 1998. Fourteen grids were established in forest fragments in the agricultural landscape. All fragments were completely isolated by agricultural fields and were ≥50 m from the next forest patch. In the agricultural landscape, grids covered the entire fragment. Seven grids in the agricultural landscape were surveyed in all years, with the remainder added in the second and third years of study (Table 1).

At each grid, song playback was used to attract males into mist nets. Once captured, all Ovenbirds received a U.S. Fish and Wildlife Service aluminum band and three leg bands made of colored plastic to form a unique band combination. Most Ovenbirds were captured within 2–3 wk after arrival from spring migration. Upon capture, right wing chord (in millimeters) and mass (in grams) were measured and the third right rectrix was plucked to determine age. Each grid was visited at least three times per season to determine the status of the Ovenbirds that were present.

The age of each Ovenbird was determined using the wear pattern of the third rectrix (Donovan and Stanley 1995), with each individual being classified as either a second-year (SY) or an after-second-year (ASY) bird. Individuals with tip angles ≤78° were classified as SY and individuals with tip angles ≥90° were classified as ASY. Using these criteria, Donovan and Stanley (1995)

TABLE 1. Landscape attributes and time period when each site in Saskatchewan was surveyed for the Ovenbird mark–recapture study.

Site	Area (ha)	Forest cover (%)	Period
Farm fragments			
Bossemaier	5	25	1996–1999
Cabin	5	64	1998–1999
Triangle 1	5	18	1997–1999
Triangle 2	5	19	1997–1999
Carruthers	7	33	1996–1999
Connolly	7	26	1996–1999
Horvath	10	22	1996–1999
Hulit	10	63	1998–1999
Church	11	16	1997–1999
Dinius	11	21	1996–1999
Dump	12	44	1998–1999
Dean	15	30	1997–1999
Bader	20	45	1996–1999
McConnell	42	22	1996–1999
Forestry fragments			
Bear	35	49	1996–1999
Clarine Lake	25	62	1998–1999
Snowfield	25	50	1996–1999
Continuous forest			
Namekus Lake		100	1998–1999
Mud Creek		100	1996–1999
Powerline		100	1996–1999

Note: The size of each fragment and the percentage of the surrounding landscape within 1 km of each fragment that was covered by forest are also provided.

accurately classified 99% of known-aged Ovenbirds. Individuals with feather tip angles that were between these values were excluded from initial analyses (Donovan and Stanley 1995). One person, with 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 times. Images were printed and the angle of the feather tip was measured using grid paper and a protractor.

As part of another study examining the effects of forest fragmentation on pairing success of male Ovenbirds, we established the pairing and/or breeding status of a subset of males. Detailed information on methods used to collect these data are given in Bayne and Hobson (2001). In brief, 164 of the banded males were followed for a period of up to 90 min to determine if a female was present on their territory. Of these males, 136 were paired and 28 were unpaired. During our pairing-success observations, we also discovered Ovenbird nests, which were monitored every 2–4 d until their fate was established. We also observed some males feeding young that had fledged, which we considered evidence of a successful nesting attempt. Based on these observations, we assessed whether return rate was influenced by the previous year's pairing status and/or nesting success.

Statistical analysis

To determine if apparent annual survival of male Ovenbirds varied within and among landscapes, we fit Cormack-Jolly-Seber (CJS) models to the mark–recapture data. CJS models estimate survival by correcting the observed return rate by the recapture probability. Recapture probability is the likelihood that a bird will be recaptured or resighted in a particular year, given that it is alive (White and Burnham 1999). For example, if a bird is initially captured in year 1, not seen in year 2, but recaptured in year 3, it had to be alive in year 2 but simply was not counted in that year. By correcting return rate for recapture probability, CJS models provide more precise estimates of survival than do simple return rates. Although CJS models correct for temporary emigration, they do not distinguish mortality from permanent emigration, and represent minimum estimators of true survival (Lebreton et al. 1993).

Maximum likelihood estimates of apparent annual survival and recapture probability were calculated with the computer program MARK (White and Burnham 1999). Using MARK, we determined if sites within each landscape had similar apparent survival and recapture estimates and could be pooled to derive more precise survival estimates. For each landscape, we began with a fully parameterized global model that included site, year, and the site × year interaction. One of the forestry fragments and one of the continuous forest sites were examined for only a 2-yr period (1998–1999); hence, we were unable to generate a recapture probability for these sites and they were initially excluded from analysis. For the global model in the agricultural landscape, site was replaced with fragment size (in hectares). Fragment size was treated as a continuous covariate. We chose to use fragment size as a continuous covariate rather than to create site-specific estimates of survival in each fragment in the agricultural landscape, because small sites had too few individuals to generate precise survival estimates. For example, the 5-ha farm fragments had a maximum of four unique individuals captured over the length of the study, which is insufficient to create a site-specific estimate of survival. To create the most parsimonious model that explained the most variation in the data, all possible combinations of independent variables were examined (Kleinbaum et al. 1988). Based on the Akaike Information Criterion corrected for small sample size (AIC_c), we selected the model that required the fewest parameters to explain the most variance (i.e., had the lowest AIC_c; Burnham and Anderson 1998). When two or more models had similar AIC_c values (<2), the model with the fewest parameters was chosen. A likelihood ratio test (LRT) was used to determine if inclusion of a particular effect resulted in a significant change in the deviance explained. For LRT testing, we compared the model that contained the effect of interest, in both the survival and recapture sides of the equation, against the model that contained the effect for survival but treated recapture as constant, and vice versa (Lebreton et al. 1992). We did not calculate apparent survival for each site in each year and use these survival values in an ANOVA (e.g., Porneluzi and Faaborg 1999), because survival estimates from the same site in different years are not independent (Lebreton et al. 1993).

For each landscape, nest success was calculated using the Mayfield method (Hensler and Nichols 1981). Mayfield estimates weight the importance of each nest, based on the stage when the nest was discovered and the number of days that the nest was observed. Daily survival probability was estimated using the 50% midway assumption, in which a nest was assumed to have fledged or been destroyed midway between subsequent visits. Insufficient data were available to generate precise Mayfield estimates for each site and year. Therefore, data were pooled among sites within landscapes. The Mayfield estimates for each landscape were compared using the program CONTRAST (Sauer and Williams 1989).

To determine if the age structure of Ovenbird populations differed among landscapes, a weighted least-squares (WLS) ANOVA was used (Neter et al. 1985). In this analysis, the dependent variable was the percentage of SY males per site in each year, whereas the independent variables were landscape and year. We used a WLS approach because the variance in the percentage of SY male Ovenbirds was inherently higher in small fragments, simply because fewer males were present in these sites (i.e., estimates of age structure

TABLE 2. Reduced *m*-array of male Ovenbirds marked and recaptured in each landscape.

Landscape and year	R_i	1997	1998	1999	r_i
Farm fragments					
1996	42	12	2	1	15
1997	60		24	2	26
1998	67			23	23
m_j		12	26	26	
Forestry fragments					
1996	47	23	2	0	25
1997	46		14	5	19
1998	62			23	23
m_j		23	16	28	
Continuous forest					
1996	52	20	4	1	25
1997	79		27	7	34
1998	71			27	27
m_j		20	31	36	
All sites					
1996	141	55	8	2	65
1997	185		65	14	79
1998	200			73	73
m_j		55	73	89	

Notes: Numbers are pooled over all sites within each landscape. R_i is the number of marked individuals released in year *i*, including newly marked and previously marked individuals. Annual values are the numbers of individuals from a given release cohort that were first recaptured in that year; r_i is the total number of individuals from a release cohort captured at least once; and m_j is the total number of recaptures in a given year.

were less precise in small than in larger fragments). Each data point was multiplied by the reciprocal of the number of individuals per site (Neter et al. 1985). A similar analysis was done to determine if the age of new recruits differed among landscapes. Recruits were defined as Ovenbirds not previously captured at sites where banding had taken place in previous years.

To determine if mass or right-wing length of male Ovenbirds differed among landscapes, we created a series of linear regression models. Independent variables included in these analyses were landscape, year, age, and all two-way interactions. Time and Julian date were also included in models for predicting mass. Because many (79%) of the returning Ovenbirds were resighted rather than recaptured, only mass and right-wing length at first capture were used in these analyses. All possible combinations of variables were examined and the model with the lowest AIC_c was selected.

A two-factor Kruskal-Wallis test was used to determine if the distance moved between subsequent capture locations differed among landscapes and for males that returned in successive years vs. males that "skipped" a year (i.e., males that were absent from sites in the year following banding, but were detected in a future year). For males that returned to a site more than once, the distances between the initial capture location and first return location were used in analyses. A Kruskal-Wallis test was also used to determine if the distance moved between successive capture locations was different between males whose nests were destroyed relative to those that fledged young. All results are means ± 1 SE unless otherwise reported.

RESULTS

Apparent annual survival

Overall, 398 male Ovenbirds were captured over the four years of study and 163 returned to the same site at least once (Table 2). In continuous forest, 151 males were captured and 67 returned to the same site at least once. For the two continuous forest sites surveyed from 1996 to 1999, we could detect no difference in apparent survival or recapture probability among sites ($\chi^2 = 1.9$, df = 1, $P = 0.17$; and $\chi^2 = 0.8$, df = 1, $P = 0.39$, respectively) or years ($\chi^2 = 0.1$, df = 1, $P = 0.76$; and $\chi^2 = 0.1$, df = 1, $P = 0.88$). Pooling data from the three continuous forest sites, apparent annual survival of male Ovenbirds was 62 ± 6%, with a recapture probability of 58 ± 8%. In forestry fragments, 116 males were captured and 50 returned to the same site at least once. For the two forestry fragments surveyed from 1996 to 1999, we could detect no difference in apparent survival or recapture probability among sites ($\chi^2 = 0.5$, df = 1, $P = 0.48$; and $\chi^2 = 1.6$, df = 1, $P = 0.21$) or years ($\chi^2 = 2.6$, df = 1, $P = 0.11$; and $\chi^2 = 4.3$, df = 1, $P = 0.12$). Pooling data from all three forestry fragments, apparent annual survival of male ovenbirds was 56 ± 6%, with a recapture probability of 70 ± 9%. In farm fragments, 131 males were captured and 46 returned to the same site at least once. The most parsimonious model indicated that fragment size was positively correlated with apparent annual survival ($\beta = 0.8$, $\chi^2 = 5.4$, df = 1, $P = 0.02$) and negatively correlated with recapture probability ($\beta = -1.8$, $\chi^2 = 8.3$, df = 1, $P = 0.004$).

Pooling all sites within a landscape to derive our survival estimates, we could not detect a difference in apparent survival of male Ovenbirds among farm fragments (49 ± 6), forestry fragments (56 ± 6), or continuous forest (62 ± 6: $\chi^2 = 1.5$, df = 1, $P = 0.48$), nor could we detect a difference in recapture probability ($\chi^2 = 0.6$, df = 1, $P = 0.73$). However, farm fragment size was an important predictor of apparent annual survival and recapture probability, suggesting that Ovenbirds in small farm fragments had lower apparent survival than in larger farm fragments. To assess the importance of fragment size, we separated the two largest sites (>20 ha) in the agricultural landscape from the 12 smaller farm fragments (<15 ha). Although this split was arbitrary, it provided two groups with approximately equal numbers of males in each category. Apparent survival of male Ovenbirds was significantly higher in the two largest farm fragments (58 ± 8%) than in the 12 smaller farm fragments (34 ± 5%: $\chi^2 = 6.0$, df = 1, $P = 0.01$). The low apparent survival of

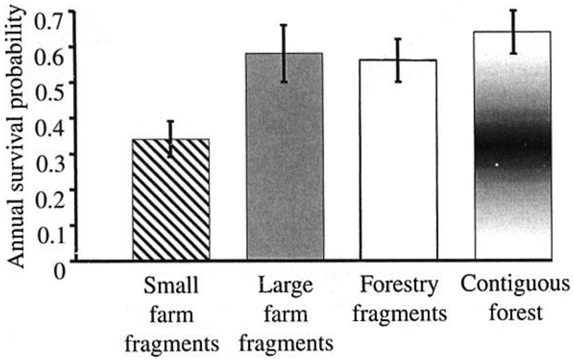

FIG. 2. Apparent annual survival probability of male Ovenbirds in each landscape. Error bars represent 95% confidence intervals for each estimate.

Ovenbirds in small farm fragments resulted, in part, from the high recapture probability in small farm fragments (100%) relative to large farm fragments (61 ± 12%: $\chi^2 = 4.7$, df = 1, $P = 0.01$). Treating the two largest fragments as a separate category, we found that apparent survival differed significantly between landscapes ($\chi^2 = 8.6$, df = 3, $P = 0.04$: Fig. 2). However, the difference in recapture probability was not significant among these four groups ($\chi^2 = 6.2$, df = 3, $P = 0.09$). The most parsimonious description of our data is that apparent survival ($\chi^2 = 8.0$, df = 1, $P = 0.005$) was significantly lower and recapture probability was significantly higher ($\chi^2 = 5.2$, df = 1, $P = 0.02$) in small farm fragments (34 ± 5) than in all other sites combined (59 ± 3).

Breeding success and return rate

Over four years, 68 Ovenbird nests were located. Brood parasitism by Brown-headed Cowbirds did not occur in the continuous forest or forestry fragments, but occurred in 17% of nests in farm fragments, with all but one nest being parasitized in 1997. Daily nest success was greatest in the continuous forest (97.9 ± 0.8%), intermediate in forestry fragments (96.7 ± 1.3%), and lowest in farm fragments (95.8 ± 1.1; Table 3). However, we could not detect a statistically significant difference in nest success among landscapes ($\chi^2 = 2.7$, df = 2, $P = 0.29$).

Using contingency table analysis, we found that the probability of a male returning in a subsequent breeding season was dependent on pairing success in the previous year ($\chi^2 = 9.4$, df = 1, $P = 0.002$). Unpaired Ovenbirds were less likely to return in a subsequent year (11% of 28 males) than were paired males (41% of 136 males). The probability that a male would return in a subsequent breeding season when his nest was destroyed (29% of 21 males) was not significantly different from that of males with successful nests or that were observed with young (46% of 50 males; $\chi^2 = 1.9$, df = 1, $P = 0.17$).

Age structure and body condition

There was some evidence that the percentage of SY male Ovenbirds in the population differed among landscapes ($F_{2,46} = 2.7$, $P = 0.08$). A larger percentage of the population in farm fragments (47 ± 4%) were SY males relative to continuous forest (37 ± 4%) or forestry fragments (33 ± 4%). This pattern was consistent over the duration of the study because year was not a significant predictor of the population age structure ($F_{2,46} = 0.6$, $P = 0.95$). However, considerable numbers (23%) of individuals had intermediate feather angles and were classified as unknowns. Differences in the age structure among landscapes were stronger when all individuals captured were classified as either SY or ASY males (SY ≤ 84° and ASY > 84°). Using the new criteria, farm fragments had a significantly greater percentage of SY males (59 ± 4%) than did forestry fragments (47 ± 4%) or continuous forest (45 ± 4%: $F_{2,47} = 4.1$, $P = 0.02$; Fig. 3A). Donovan and Stanley (1995) found that, using this less stringent classification, 90% of known-aged birds were classified accurately.

The percentage of SY Ovenbirds recruited into the population differed among landscapes ($F_{2,25} = 5.9$, $P = 0.009$). More SY males were recruited into farm fragments (90 ± 5%) than forestry fragments (73 ± 5%) or continuous forest (70 ± 4%). This pattern remained when the less stringent age classification was used, as farm fragments had a significantly greater percentage of SY recruits (90 ± 5%) than forestry fragments (74 ± 5%) or continuous forest (64 ± 4%; $F_{2,26} = 9.4$, $P = 0.001$; Fig. 3B).

Controlling for the other variables retained in the models, we detected no differences in mass ($F_{2,398} = 1.5$, $P = 0.22$) or wing length ($F_{2,398} = 0.1$, $P = 0.92$) of male Ovenbirds in the different landscapes (Table 4). Mass at first capture was different among years ($F_{2,398} = 5.1$, $P = 0.007$). The interacting effect of year and landscape on mass was also significant ($F_{6,398} = 3.0$, $P = 0.007$), although no clear trend existed in the data (Table 4). Mass at first capture was positively correlated with time of day ($\beta = 0.24$, $F_{1,398} = 24.5$, $P < 0.001$) and Julian date ($\beta = 0.18$, $F_{1,398} = 11.0$, $P < 0.001$). Age was not related to mass ($F_{1,398} = 0.7$, $P = 0.42$). In contrast, ASY males had slightly longer primary feathers than SY males (76.9 ± 0.1 mm vs.

TABLE 3. Number of Ovenbird nests located in each landscape and the fate of those nests. Daily survival probability (±1 SE) is based on a Mayfield estimate.

Landscape	Fledged young	Destroyed	Exposure days	Daily survival probability
Farm fragments	14	15	358	0.958 ± 0.011
Forestry fragments	11	6	180	0.967 ± 0.013
Continuous forest	15	7	326	0.979 ± 0.008

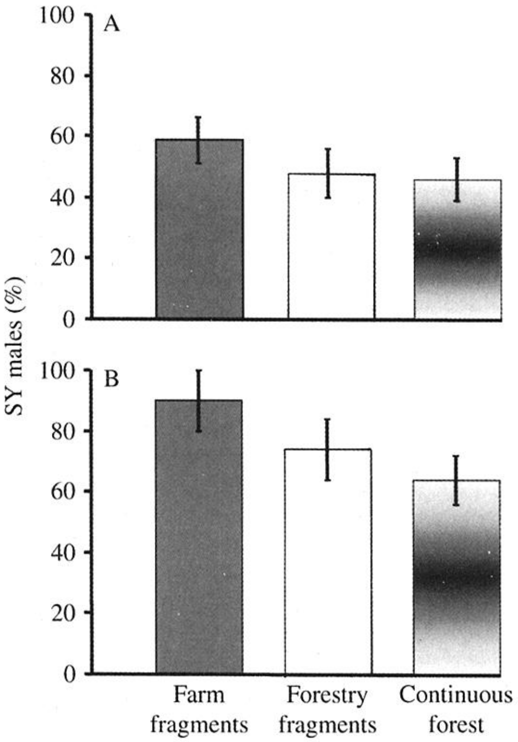

FIG. 3. Mean percentage (weighted least-squares means) in each landscape of: (A) the total Ovenbird population that were second-year (SY) males; and (B) recruits that were SY males. Recruits were unbanded individuals captured at sites where banding had taken place in previous years. Error bars represent 95% confidence intervals. SY males had a third rectrix with a tip angle of ≤84°.

76.0 ± 0.2 mm, respectively; $F_{1,398} = 5.2$, $P = 0.02$). Correcting mass for wing length, time of day, and date measured, we observed no differences in body condition among landscapes ($F_{2,398} = 1.8$, $P = 0.16$), although body condition differed among years ($F_{2,398} = 4.6$, $P = 0.01$). The interacting effect of landscape and year also affected body condition ($F_{6,398} = 2.9$, $P = 0.008$), although no clear trend existed.

Distances between subsequent territories

There was no difference in the median distance moved between subsequent capture locations for males that returned in successive years (50 m; range 10–300 m, $n = 136$) vs. males that skipped a year (60 m; range 10–250 m, $n = 24$, $H = 0.55$, $P = 0.47$). Most returning males (88%) were relocated <100 m from their location in previous years. There was no difference among landscapes in the distance moved by returning males ($H = 0.68$, $P = 0.88$). Median distance moved by males whose nests were destroyed (30 m; range 10–100 m, $n = 9$) vs. males that fledged young (50 m; range 10–280, $n = 23$) was also not different ($H = 2.2$, $P = 0.14$).

DISCUSSION

Apparent annual survival of male Ovenbirds was lower in small farm fragments than in all other landscapes. We suspect that low reproductive success in small farm fragments resulted in increased dispersal from this habitat relative to the other landscapes, rather than adult mortality being higher in small fragments. In support of such a dispersal hypothesis, males that fledged young were more likely to return in a subsequent year than males that failed to raise young. Unpaired males seemed most likely to disperse, as they had an apparent annual survival probability of only 11%. Males that fledged young tended to return more often than males whose nests failed, although this difference was not statistically significant. In Missouri, Porneluzi and Faaborg (1999) found that 41% of Ovenbird males observed with fledglings returned the next year, whereas only 10% of males not observed with fledglings returned. In Saskatchewan, some of the males whose nests were destroyed may have returned in subsequent years because a later nesting attempt was successful.

Ovenbirds with a lower probability of reproducing may also have been in poorer body condition, and therefore more likely to die between breeding seasons (Haas 1998). However, this does not seem to be a likely

TABLE 4. Mean (± 1 SE) wing length, mass, and body condition for second-year (SY) and after-second-year (ASY) male Ovenbirds in each landscape.

Landscape and age class	No. males measured	Wing length (mm)	Mass (g)	Body condition†
Farm fragments				
SY	96	76.2 ± 0.20	19.0 ± 0.11	−0.15 ± 0.10
ASY	35	76.9 ± 0.45	19.2 ± 0.19	−0.01 ± 0.16
Forestry fragments				
SY	74	76.3 ± 0.23	19.1 ± 0.12	−0.09 ± 0.13
ASY	42	76.8 ± 0.39	19.3 ± 0.14	0.02 ± 0.14
Continuous forest				
SY	94	76.3 ± 0.19	19.3 ± 0.10	0.09 ± 0.10
ASY	57	76.6 ± 0.29	19.4 ± 0.12	0.19 ± 0.12

† Body condition values were the residuals from a linear regression model correcting mass for time when captured, date captured, and wing length.

explanation for our results, as we observed no differences in body condition for paired vs. unpaired males (Bayne and Hobson 2001) or among males in the different landscapes. Alternatively, Ovenbirds in small farm fragments may have experienced increased overwinter mortality because of energetic stresses caused by renesting (Haas 1998). However, unpaired males probably expended less energy than breeding males because they did not have to care for young, yet they almost never returned.

Dispersal from sites was not always permanent. The probability of recapturing Ovenbirds in each landscape ranged from 60% to 100%. In continuous forest, males that were not recaptured every year may have been present, but missed, because of small changes in territory location (e.g., they moved just off the grid). It is unlikely that males were missed in large farm or forestry fragments; changes in territory location among years would not influence the recapture/resighting probability because the entire forest patch was searched at least three times. In addition, the numbers of Ovenbirds present on each grid each year were similar, suggesting that we had accounted for all males present. That male Ovenbirds did not have perfect recapture probabilities suggests that some individuals dispersed to new breeding sites and then, for whatever reason, returned to sites where they had previously bred (Lebreton et al. 1993).

Increased immigration into small farm fragments by young males seemed to compensate for the low return rate to small fragments. High turnover of males in small farm fragments influenced the age structure of the population, as young males made up a larger percentage of the population in small farm fragments than in the other landscapes. Possibly, older males in larger forest stands forced young Ovenbirds to breed in small farm fragments by preemptive territory selection in continuous forest (Holmes et al. 1996). Alternatively, young males with no prior breeding experience may not have recognized the lower suitability of small farm fragments and simply filled vacancies left by males that did not return to sites where breeding success was low (Wilcove 1985).

Where Ovenbirds that dispersed from small fragments went in subsequent years is unknown. Ovenbirds may have "learned" that small fragments were poor-quality habitat and may have sought territories in continuous forest. Alternatively, Ovenbirds may be "hardwired," automatically dispersing after failed breeding attempts and filling any available breeding habitat that they encounter. Males colonizing territories in continuous forest tended to be older, suggesting that males from small forest fragments dispersed to continuous forest in subsequent years. However, whether this represents "learning" is unclear because the continuous forest and agricultural landscape in this study were close together. Thus, dispersing individuals from small farm fragments had a relatively high probability of randomly encountering continuous forest. In addition, nonterritorial floaters were more common in our continuous forest sites than in farm fragments (Bayne and Hobson 2001). The larger percentage of ASY males recruited into continuous forest populations could have resulted from floaters obtaining territories as they get older, rather than from failed breeders dispersing from the small farm fragments to the larger forest blocks (Sherry and Holmes 1989).

Although we had insufficient nests to statistically demonstrate reduced nesting success in the agricultural landscape, our data are consistent with other studies arguing that forest fragmentation reduces nesting success of Ovenbirds (Robinson et al. 1995). A larger data set from 12 species of songbirds and an artificial nest study conducted in our study area support this conclusion; both found significant differences in nest success between fragments in the agricultural landscape relative to continuous forest (Bayne and Hobson 1997, Hobson and Bayne 2000*a*). These results suggest that increased dispersal of male Ovenbirds from small farm fragments may be driven in part by high nest predation. Assuming that nest predation is a key determinant of breeding dispersal, populations of Ovenbirds in other fragmented regions may be even more prone to disperse. In a large-scale study across the midwestern United States, Robinson et al. (1995) found that daily nest survival in continuous forest was similar to what we observed in the boreal forest (~0.97 vs. 0.98, respectively). In contrast, daily nest survival in landscapes with ~30% forest cover was considerably lower in the American midwest (~0.93) than in our fragmented agricultural landscape (0.96).

The impacts of anthropogenic fragmentation in forested landscapes on Ovenbird demography probably depend on the type, amount, and time since disturbance. Similar to our results, studies in mature forestry fragments surrounded by regenerating clearcuts often have found no differences in density, pairing success, or nesting success of Ovenbirds relative to continuous forest (King et al. 1996, Sabine et al. 1996, Lambert and Hannon 2000). In contrast, Ovenbird density and pairing success tended to be lower within 150 m of gravel roads relative to forest interiors in Vermont (Ortega and Capen 1999). In Maine, Ovenbirds holding territories in forest stands adjacent to clearcuts created in the preceding winter suffered low pairing success relative to Ovenbirds occupying stands in unharvested areas, because of increased territorial competition from Ovenbird males that were displaced by timber harvesting (Hagan et al. 1996). Clearly, forestry activities can affect Ovenbird demography, but whether these effects persist in the long term is not clear. Unlike agricultural landscapes where fragmentation effects are permanent and change predator communities, the effects of fragmentation caused by harvesting may be more ephemeral and less likely to increase nest predation (Rudnicky and Hunter 1993, Bayne and Hobson 1997).

Forest fragmentation is having negative impacts on Ovenbird populations in many areas of North America (Donovan et al. 1995*b*, Porneluzi and Faaborg 1999). Increasing nest predation and cowbird parasitism has created vast areas of sink habitat where breeding productivity seems to be insufficient to compensate for adult mortality. However, many highly fragmented areas still support high densities of Ovenbirds. The observation of more SY Ovenbirds in small farm fragments than in the other landscapes suggests that Ovenbird populations in small farm fragments are being rescued by immigration of excess juveniles produced in other less fragmented areas. The larger number of ASY recruits in continuous forest in our study area also suggests that failed breeders from small farm fragments may be dispersing to continuous forest. However, the continuous boreal forest is a heterogeneous system with a wide variety of forest stand types, many of which are utilized by Ovenbirds (Hobson and Bayne 2000*b*). Variation in site quality associated with stand type undoubtedly influences Ovenbird demography, such tha some of the dispersal/recruitment patterns that we observed might also be occurring at a smaller scale within a landscape. Regardless, our results suggest that conversion of forest to agricultural land and the resulting fragmentation of the remaining forest habitat are having negative consequences for Ovenbirds and probably many other species of forest songbirds.

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