MOVEMENT PATTERNS OF ADULT MALE OVENBIRDS DURING THE POST-FLEDGING PERIOD IN FRAGMENTED AND FORESTED BOREAL LANDSCAPES[1]

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Abstract. Movement of forest songbirds among isolated forest patches following breeding represents an important but poorly understood component of landscape ecology and metapopulation theory. Using radio-telemetry, we followed 44 male Ovenbirds (*Seiurus aurocapillus*) during the post-fledging period to determine if movement patterns differed in landscapes dominated by agriculture versus those dominated by forest. No differences in home-range size, mean distance moved per day, or maximum distance moved were observed for males captured in a forested landscape vs. those captured in forest fragments in an agriculturally dominated landscape. Male Ovenbirds observed with young moved less than males without young and rarely crossed open gaps. Individuals that failed to breed moved more extensively than successful breeders, possibly in an effort to find new territories for use in future breeding seasons.

Key words: boreal forest, dispersal, fragmentation, gap crossing, movement, Ovenbird, Seiurus aurocapillus.

Patrones de Movimiento de Machos Adultos de *Seiurus aurocapillus* Tras la Salida de los Pichones del Nido en Paisajes Boreales Fragmentados y Boscosos

Resumen. Los movimientos de las aves canoras entre parches aislados de bosque tras la reproducción representan un importante pero poco entendido componente de la ecología del paisaje y la teoría de metapoblaciones. Usando radiotelemetría, seguimos 44 *Seiurus aurocapillus* durante el período posterior a la salida de los pichones del nido para determinar si existían diferencias en los patrones de movimiento de estas aves entre paisajes dominados por agricultura y paisajes dominados por bosques. No encontramos diferencias entre machos adultos capturados en un paisaje boscoso y en fragmentos de bosque inmersos en un paisaje dominado por sistemas agrícolas en términos del tamaño del área de hogar, la distancia promedio recorrida diariamente ni la máxima distancia recorrida. Los machos observados en compañía de pichones se movieron menos que aquellos sin pichones y raramente cruzaron claros abiertos. Los individuos que no lograron reproducirse se movieron más que aquellos que tuvieron éxito en la reproducción, posiblemente buscando nuevos territorios para utilizar en épocas reproductivas futuras.

INTRODUCTION

Isolation of forest fragments influences the composition of forest songbird communities (Robbins et al. 1989, Freemark and Collins 1992). However, the mechanisms determining whether a species is present in an isolated forest fragment remain unclear. It is often assumed that the matrix of open habitats in which forest fragments exist acts as a barrier to movement that limits the ability of birds to colonize isolated areas (Whitcomb et al. 1981, Lynch and Whigham 1984). Although the ability of individuals to move among fragments is key to the persistence of forest songbird metapopulations (Villard et al. 1995), how habitat gaps influence forest songbird movements is poorly understood (Desrochers and Hannon 1997, Cassady-St. Clair et al. 1999, Grubb and Doherty 1999).

Between fledging and migration, territoriality in many songbirds breaks down and individuals
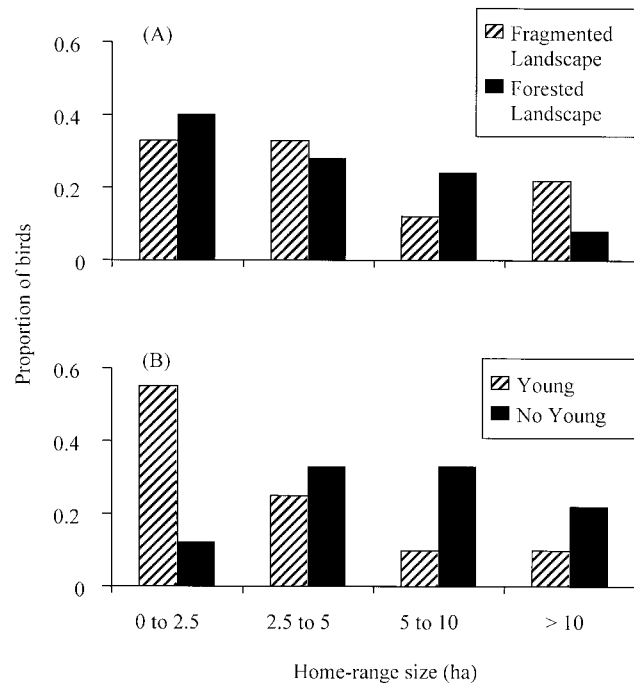
FIGURE 1.   Distribution of male Ovenbird home-range sizes in July 1997 and 1998 in Saskatchewan, Canada. Home-range size was calculated as 95% minimum convex polygon using all data points for each individual. Home-range size: (A) in fragments ($n = 19$) and continuous forest ($n = 25$); (B) for individuals with young ($n = 22$) versus those without young ($n = 22$).

begin to move widely (Cherry 1985, Vega Rivera et al. 1999). During this post-fledging period, habitat fragmentation may limit the movements of juveniles, family groups, and even adults. For example, the dispersal of juvenile Crested Tits (*Parus cristatus*) out of forest fragments was delayed relative to individuals from a forested landscape, and this was attributed to a reluctance of juveniles to cross open areas (Lens and Dhondt 1994). Juvenile and adult songbirds in a landscape fragmented by forestry tended to move through forested corridors rather than across open clearcuts (Machtans et al. 1996). Matthysen et al. (1995) found adult European Nuthatches (*Sitta europaea*) in small forest fragments were less likely to disperse to a new territory in a subsequent year than individuals in a forested landscape. Together, these studies suggest that forest fragmentation reduces the mobility of forest songbirds following breeding, and may act as a limit to dispersal (Opdam 1991).

We used radio-telemetry to compare the post-fledging movements of adult male Ovenbirds (*Seiurus aurocapillus*) captured in forest fragments in a landscape dominated by agriculture to those of individuals captured in a forested landscape. To determine whether movements of failed and successful breeders were differentially affected by forest fragmentation, movement patterns were compared between males seen with young versus those not seen with young.

METHODS

The study was conducted in Prince Albert National Park (PANP, 53°50′N, 105°50′W) and the adjacent rural municipality of Paddockwood (53°31′N, 105°34′W; see Fig. 1 in Bayne and Hobson 1997) in Saskatchewan, Canada. PANP is a 387 500-ha area of mostly mature forest, containing one small town, four major road corridors, and two major powerline corridors. The rural municipality of Paddockwood is a highly fragmented landscape dominated by agriculture, and as measured from LANDSAT imagery has only about 23% forest cover (Hobson et al., unpubl. data). The study was conducted in July 1997 and 1998 in mature to old (60 to 100 years)

mixedwood forest dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). Sites were selected from 1:12 500 aerial photo and forest inventory maps, based on similar tree composition, age, and lack of disturbance (e.g., cattle grazing or selective timber harvest).

In sites within each landscape, we created flagged grids that consisted of 50 × 50 m cells. In the forested landscape, we used four 16-ha grids, while in the fragmented landscape we used seven fragments ranging in size from 6 to 30 ha (mean 14 ± 8 ha). In the fragmented landscape, flagged grids covered the entire study fragment. Canola or wheat fields isolated fragments, with at least 50 m separating adjacent fragments. The minimum distance between sampled forest fragments was 2 km, while sites in the forested landscape were at least 5 km apart.

At each grid in each year, one to six male Ovenbirds were captured using song playback to draw individuals into mist nets (Bayne 2000). All individuals captured were adult males. Individuals were captured between July 2 and July 17, with most individuals captured within a week of the mean fledging date. Ovenbirds had not been observed before capture, so breeding status was unknown initially. We relied on observations of young accompanying radio-fitted birds to indicate whether males were successful in breeding that year. Using this method we could not determine whether birds without young were unpaired, floaters, had suffered a nest failure, or were successful breeders that had left the family group. However, because the study began just after the mean fledging date (Bayne 2000), we feel it is unlikely that all individuals without young had left their fledglings and believe that most suffered some type of reproductive failure that year.

Each individual was fitted with a Holohil Ltd. (112 John Cavanaugh Road, Carp, Ontario) BD2-A radio-transmitter, weighing 0.6 g (3% of adult Ovenbird body mass). Transmitters had a range of about 800 m. The manufacturer-suggested battery life for the transmitters was four weeks (but see below). For 40 individuals, the transmitter was affixed to feather stubs using epoxy (Warnock and Warnock 1983), while a backpack harness made of elasticized yarn was used on 18 individuals (B. Woolfenden, pers. comm.). Both techniques were employed each year. To allow individuals time to adjust to the transmitters, the first observations were not recorded until 24 hr after transmitter attachment.

Each individual was located one to two times daily using a handheld receiver and a four-element Yagi antenna. Locations were pinpointed by approaching each individual until it was seen. Once individuals were located visually, they were followed for about 0.5 hr to determine whether young were present. Locations were marked on maps created for each site and entered into the geographic information system Arcview 3.1. When Ovenbirds moved off grids, a Trimble global positioning system accurate to ±10 m was used to determine the geographic coordinates of new locations.

When a signal could not be located, we drove or walked 3-km transects in the four cardinal directions from the last known location. Attempts were made to locate individuals for about four days after last contact. In most cases, we could not determine whether Ovenbirds had left the study area or whether the transmitter had failed. Most signal losses occurred within three weeks of radio-transmitter activation, which seemed to be the average life span of the transmitters.

Using the program Animal Movement (Hooge and Eichenlaub 1997), home-range size (95% minimum convex polygon) was calculated for Ovenbirds tracked for at least seven days. Ovenbirds were often relocated more than once per day and we based the 95% minimum convex polygon on all points. All observations within the same day were separated by at least 2 hr. However, the statistical independence of locations within the same day has been questioned (White and Garrott 1990, but see De Solla et al. 1999), so we also calculated a 95% minimum convex polygon based on the first observation each day. The conclusions from the two methods did not differ, so we report only the results of the 95% minimum convex polygon using all points. For each individual, mobility (mean distance between daily locations), maximum distance moved (distance between two most extreme points), and whether it crossed a gap (nonforested area greater than 25 m wide) was also calculated. Data were analyzed in two ways. Using natural-log transformed values, a nested analysis of covariance (ANCOVA) was calculated using individual movements as subsamples within a site. We chose to use a nested design because individuals within sites are not neces-

sarily biologically or statistically independent. Sites sampled in both years were treated as independent (two sites in each landscape), as the individuals tracked were different between years. The model we fit to the data included landscape, breeding status (with or without young), the interaction term landscape × breeding status, attachment method (harness or glue), and site (statistically nested with landscape). The number of days tracked was entered as a continuous covariate. Because of concerns with normality, we also analyzed the data with nonparametric Kruskal-Wallis tests using each individual as an independent replicate.

For Ovenbirds captured in fragments, nearest-neighbor analysis (Hooge and Eichenlaub 1997) was used to determine if the locations of each individual within fragments were clustered or randomly spaced across the fragment. For Ovenbirds that left the fragment of capture, the site where they spent the most time was used for these analyses. To determine if Ovenbirds avoided edges of fragments, 25- and 50-m wide buffers within the perimeter of each fragment were created analytically and the proportion of locations within each buffer calculated. Observed patterns of edge use in each fragment were compared to five theoretical home ranges generated for each fragment. Theoretical home ranges were created by randomly generating 18 locations (the average number of locations obtained) within each fragment. To determine if Ovenbirds avoided or utilized edges more or less than randomly created home ranges, we used a nested ANOVA with site nested within home-range type (real vs. theoretical). To determine if the size of fragments was the cause of the site effect (see Results), we also used an ANCOVA where the nested site term was replaced by the area of the fragment (ha). The proportion of locations within each edge buffer was arcsine transformed prior to analysis. Data are reported as means ± SD unless otherwise indicated.

RESULTS

Overall, 58 male Ovenbirds were captured and fitted with radio-transmitters, 27 in fragments and 32 in the forested landscape. Fourteen Ovenbirds lost their transmitters in less than a week and were not included in our analyses. Predators killed three individuals. Of the 44 Ovenbirds followed for more than a week, 25 were captured in the forested landscape (15 with young and 10

without young) and 19 (7 with young and 12 without young) were captured in fragments. On average, 2.0 ± 1.0 (range 1 to 4) males per year were followed in each fragment. In the forested landscape, 4.2 ± 1.9 (range 1 to 6) males per year were followed at each site. Transmitter life was shorter than expected. Three transmitters that fell off Ovenbirds and were recovered lasted only 19 to 23 days. This made it difficult to determine how many individuals left the study area during the period of observation. However, two Ovenbirds went missing well before the average life of transmitters was reached.

There was no evidence that the number of days tracked influenced the size of any of the movement parameters in the nested ANCOVA models (all $P > 0.20$). Also, none of the movement parameters were correlated with the number of days tracked using Spearman rank correlation tests (all $P > 0.20$). Method of attachment (epoxy or harness) had no effect on the movement patterns in the nested ANCOVA model (all $P > 0.30$) or in single-factor Kruskal-Wallis tests (all $P > 0.10$). Of the four Ovenbirds that permanently left fragments, two had transmitters attached with epoxy and two had harnesses. However, all three individuals killed by predators had radio-transmitters attached with harnesses.

Males without young were more likely (83%, $n = 12$) to cross gaps in the fragmented landscape than males with young (14%, $n = 7$; two-tailed Fisher exact test, $P < 0.01$). Of the 19 males in fragments, four permanently left the fragments where they were captured and moved to two or more fragments. The maximum distance moved by these four individuals was 1056, 1380, 1740, and 5630 m. The minimum width of the gaps crossed by these individuals ranged from 100 to 300 m. These four males were never seen with young. Six males left the fragment where they were captured, crossed an area of cropland of at least 50 m to an adjacent fragment, and returned on a subsequent day. Only one of these males was seen with young. In the forested landscape, there was no difference in the frequency with which males with young (33%, $n = 15$) and males without young (30%, $n = 10$: $P > 0.50$) crossed small (<25 m wide) roads or powerlines.

Home-range size ($F_{1,23} = 0.7$, $P > 0.40$), maximum distance moved ($F_{1,23} = 2.4$, $P > 0.10$), and mobility ($F_{1,23} = 0.6$, $P > 0.40$) were not

significantly different among landscapes, based on the nested ANCOVA models (Table 1 and Fig. 1a). Males not seen with young had significantly larger home ranges ($F_{1,24} = 6.1$, $P < 0.05$), maximum distance moved ($F_{1,24} = 7.2$, $P < 0.01$), and mobility ($F_{1,24} = 5.6$, $P < 0.05$) than males seen with young (Table 1 and Fig. 1b). The interaction between landscape and breeding status was not significant for any movement parameters in the nested ANCOVA models (all $P > 0.30$). In the fragmented landscape, there was no difference in the size of fragments where we located males with young (16.5 ± 3.0 ha) vs. males without young (15.7 ± 2.1 ha: $F_{1,16} = 0.1$, $P > 0.50$). Similar results were obtained when we used two-factor Kruskal-Wallis tests with each individual as the independent unit of measurement (Table 1).

Males with young (6 of 7) tended to have more clustered patterns of habitat use in fragments than those without young (4 of 12: two-tailed Fisher exact test, $P = 0.06$). In the fragmented landscape, there was no difference in the size of fragments where we located males with young (16.5 ± 3.0 ha) vs. males without young (15.7 ± 2.1 ha: $F_{1,16} = 0.1$, $P > 0.50$). All Ovenbirds in the forested landscape showed clustered patterns of habitat use, simply because the forest patches as defined by forest inventory maps were so large (474 to 3261 ha). Using the arbitrary boundaries of our flagged grids as the borders of patches in the forested landscape, we still found that all Ovenbirds in this landscape showed clumped patterns of habitat use.

Ovenbird males did not avoid edges. In fact, the percentage of radio-tracked positions within 50 m of an edge (75 ± 19%) was greater than expected if males randomly used fragments (58 ± 13%: $F_{1,18} = 17.5$, $P < 0.001$). The proportion of radio-tracked positions within 25 m of an edge (46 ± 27%) was also greater than expected if males used fragments randomly (30 ± 12%: $F_{1,18} = 5.8$, $P < 0.05$). The nested site term was significant for both the 25-m ($F_{13,38} = 2.2$, $P < 0.05$) and 50-m buffers ($F_{13,38} = 2.6$, $P < 0.01$). Area of fragments did not explain the site effect for the 25-m buffer ($F_{1,50} = 0.1$, $P > 0.50$), but may have explained some of the site effect for the 50-m buffer ($F_{1,50} = 2.9$, $P = 0.10$). Males without young tended to have a greater percentage of observations within 50 m of edges (80 ± 17%) than males observed with young (65 ± 21%: $F_{1,9} = 3.4$, $P = 0.10$). In contrast, no dif-

ference was detected for males with and without young in the proportion of observations within 25 m of an edge ($F_{1,9} = 0.4$, $P > 0.50$).

DISCUSSION

Most male Ovenbirds remained within a few hundred meters of their capture location for the observation period regardless of landscape. In particular, males with young remained clustered in a 2- to 3-ha area around their capture point, suggesting they remained near their breeding territory. Radio-telemetry on male Ovenbirds during the nesting phase suggests that average home-range size in fragments (1.8 ± 0.8 ha) and the forested landscape (1.6 ± 0.4 ha) were similar to those of Ovenbirds observed with young in the post-fledging period (Bayne 2000). In contrast, Ovenbirds observed without young had larger home-ranges than males with young, although the movements of these individuals were similar between landscapes.

Ovenbirds crossed gaps frequently, but gap-crossing propensity depended on landscape and the presumed reproductive status of each individual. Individuals without young crossed gaps in the fragmented landscape more than males with young. Whether males with young were reluctant to move across gaps in the fragmented landscape because of predation risk to young or whether young constrained the movements of adults is unclear. Males with young in the forested landscape had similar movement patterns to those with young in the fragmented landscape. However, males with young in the forested landscape crossed small gaps created by roads and powerlines, whereas males with young in fragments rarely left the fragment, suggesting that larger gaps and open fields may be perceived as having greater risk than powerline or road gaps. Alternatively, males feeding young may have been unwilling to cross the large gaps in the fragmented landscape because of the energetic costs of commuting large distances. Although gap-crossing propensity was different among landscapes, male Ovenbirds with young had similar movement patterns between landscapes, suggesting fragmentation did not constrain the movement patterns of successful breeders.

Open farmland did not appear to be a barrier to movement for Ovenbirds without young. Long-distance movements by males without young suggest that adult dispersal may not be

TABLE 1. Movement parameters (mean, 95% CI, median, and range) for male Ovenbirds captured in forest fragments versus sites in a heavily forested landscape and for individuals with young versus those without young. P-values from nested ANCOVA models are provided beside means. P-values from two-factor Kruskal-Wallis tests are provided beside medians. n is the number of individual male Ovenbirds in each category.

Movement parameter	Fragmented landscape (n = 19)	Forested landscape (n = 25)	P	With young (n = 22)	Without young (n = 22)	P
Home-range size (ha)[a]						
Mean (95% CI)[b]	5.4 (3.1–9.5)	3.3 (2.0–5.4)	>0.40	2.2 (1.2–3.8)	7.2 (4.2–12.3)	<0.05
Median (range)	3.3 (0.8–238)	2.8 (1.1–50.4)	>0.50	1.9 (1.1–14.2)	5.7 (0.8–238.4)	<0.001
Maximum distance moved (m)						
Mean (95% CI)[b]	537 (388–742)	346 (259–461)	>0.10	270 (196–374)	639 (471–868)	<0.01
Median (range)	422 (180–5630)	290 (185–1946)	>0.50	255 (185–750)	503 (180–5630)	<0.001
Distance per day (m)						
Mean (95% CI)[b]	135 (102–176)	111 (87–141)	>0.40	87 (67–114)	160 (124–206)	<0.05
Median (range)	107 (58–659)	106 (58–265)	>0.50	141 (58–199)	159 (68–659)	<0.001
Number of relocations						
Median (range)	17 (9–35)	16 (7–52)		19 (7–52)	16 (8–31)	
Number of days tracked						
Median (range)	13 (7–20)	13 (7–23)		14 (7–23)	11 (7–18)	

[a] Calculated as 95% minimum convex polygon using all locations for each individual. Calculating home-range size from a single observation per individual per day did not change conclusions.

[b] Least-square means controlling for other variables in nested ANCOVA model. Calculated by back-transforming ln-values.

constrained by fragmentation. However, even though Ovenbirds are capable of crossing gaps, they may preferentially move through forested environments when dispersing. Cassady-St. Clair et al. (1999) found that Black-capped Chickadees (*Poecile atricapilla*) crossed open spaces of over 200 m if no other choice was available, but were unwilling to cross gaps of 50 m when alternate routes through forest were present. Similarly, Haas (1995) found that the American Robin (*Turdus migratorius*), an edge-adapted species, preferentially moved among sites connected by wooded corridors.

Ovenbirds in fragments did not avoid edges during the post-fledging period. In fact, males seemed to spend more time than expected near the edges of fragments. This pattern of edge use contrasts with the results of other studies done during the nesting period, which demonstrate the density of male Ovenbirds is lower near edges (Van Horn et al. 1995, Ortega and Capen 1999). Machtans et al. (1996) found that the number of dispersing birds captured in mist nets was greater along the edges of buffer strips than in interior habitat, and suggested that birds moved laterally along edges rather than crossing the edge and entering a clearcut. Possibly, greater edge use by Ovenbirds in fragments can be attributed to such a barrier effect (Opdam 1991).

The wider range of movements of male Ovenbirds without young could be caused by several factors. Post-breeding movement may be a strategy for finding areas of high food availability (Cherry 1985, Rappole and Ballard 1987). Alternatively, Ovenbirds may seek out areas with greater vegetation density to reduce predation risk associated with their prebasic molt. Vega Rivera et al. (1999) argued that adult Wood Thrushes (*Hylocichla mustelina*) left territories during the post-breeding period in order to search for "safe havens" where the density of vegetation was greater. Of the Ovenbirds that permanently left fragments in our study, all four were last seen in areas of dense deciduous vegetation where the forest canopy was less than 5 m high.

Although evidence is limited, migratory passerines may select future breeding territories before fall migration (Brewer and Harrison 1975, Morton et al. 1991). Thus, Ovenbirds without young may also have been "prospecting" for new territories (sensu Morton 1992), while males with young may have been reluctant to leave territories where they were successful. Little is known about adult dispersal in passerine birds, but birds that fail to raise young at a site are less likely to return to that site than birds that raise young (Haas 1998, Porneluzi and Faaborg 1999, Bayne 2000). Our results are similar to those of Vega Rivera et al. (1999) who found 64% of adult Wood Thrushes that failed to raise young left territories during the post-breeding phase, while only 25% that raised young left territories during the same period. However, the breeding status of radio-tracked individuals in our study was not known before capture. Possibly, individuals not seen with young had separated from their fledglings when captured. Once young are independent, all adult Ovenbirds may move extensively and be willing to cross gaps.

Adult Ovenbirds moved across gaps of several hundred meters, and some individuals moved extensively throughout fragmented or forested landscapes, suggesting dispersal of male Ovenbirds without young is not constrained by forest fragmentation. Thus, Ovenbirds should be able to colonize isolated fragments that have undergone local population extinction. However, point-counts in our fragmented landscape indicate Ovenbirds are often absent from isolated patches (Hobson and Bayne 2000). Ovenbirds may be more reluctant to cross open space in landscapes where the interpatch distance is greater, reducing the probability that new individuals locate isolated patches. In turn, Ovenbirds in isolated fragments may have lower reproductive success than individuals in areas of more continuous habitat (Donovan et al. 1997). Consequently, Ovenbirds may be less likely to return to isolated forest patches, increasing the likelihood that small populations in these habitats will go extinct. Metapopulation models attempting to predict the occurrence or abundance of birds in fragmented landscapes should account for the possibility that dispersal in forest birds is driven by past reproductive success. The linkages between reproductive success, dispersal, and landscape fragmentation are complex. However, that the reproductive success of many forest songbirds is lower in small, isolated forest fragments (Donovan et al. 1995, Robinson et al. 1995, but see Haas 1997) suggests that the propensity of many forest songbirds to disperse may be higher in fragmented landscapes than in more forested areas.

ACKNOWLEDGMENTS

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