Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations

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Efficient dispersal is critical to metapopulation persistence in fragmented landscapes. Yet, this phenomenon is poorly understood because it is difficult to study. We used an indirect method, experimental translocation, to investigate the permeability of three landscape types of the boreal mixedwood forest region of Canada to movements of a forest specialist, the ovenbird (*Seiurus aurocapillus*), and a habitat generalist, the white-throated sparrow (*Zonotrichia albicollis*). We captured a total of 148 males (84 ovenbirds; 64 sparrows), which were then colour banded and displaced ca. 2 km away from their territories in landscapes fragmented either by agriculture, timber harvesting, or natural disturbances. We measured the probability and time of return of individuals to their territories during the 48 h following their translocation. We examined the relative influence of landscape type, territory quality, and age, physical characteristics, and pairing status of individuals on their probability or time of return. For both species, landscape type was the only significant predictor of the probability and time of return of individuals. For the ovenbird, the agricultural landscape was least permeable, followed by the harvested and naturally patchy landscapes. The agricultural and harvested landscapes were equally permeable to white-throated sparrow movements, and the naturally patchy landscape was the least permeable. Permeability to ovenbird movements increased with the proportion of forest in the landscape. Because matrix type and the proportion and configuration of forest differed significantly among the three landscape types, we could not determine their relative influence on landscape permeability to bird movements. However, our results do indicate that even a long-distance migrant such as the ovenbird can move more rapidly and efficiently across the landscape as the proportion of suitable (or permeable) habitat increases.

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Central to the field of landscape ecology is the concept of connectivity, i.e. the degree to which landscape structure facilitates movements of organisms among resource patches (Merriam 1991, Taylor et al. 1993). Structural connectivity, or connectedness (Baudry and Merriam 1988), is the degree of physical connection (or contiguity) among habitat patches measured in the landscape irrespective of the requirements of particular organisms. Functional connectivity refers to a species-specific behavioural response to landscape structure (Tischendorf and Fahrig 2000). In this study, we relate both aspects

of connectivity by comparing the permeability of three landscape types with contrasting structures (or structural connectivity) and by measuring the behavioural response (functional connectivity) of two forest bird species with contrasting habitat requirements.

In highly fragmented landscapes, bird populations are generally structured as metapopulations (Verboom et al. 1991, Villard et al. 1995, Porneluzi and Faaborg 1999), i.e. assemblages of spatially discrete subpopulations connected by dispersal (Hanski and Gilpin 1997). Several empirical studies suggest that adults and juveniles of

various forest bird species are reluctant to cross wide gaps of open habitat (Stouffer and Bierregard 1995, Machtans et al. 1996, Sieving et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998, Brooker et al. 1999). This suggests that functional connectivity may be especially low in highly fragmented landscapes.

The influence of landscape structure on the distribution and abundance of forest birds in fragmented landscapes (reviewed by Mazerolle and Villard 1999) may partly reflect the relative permeability of the matrix to movements, which may ultimately prevent the colonization of isolated patches (Verboom et al. 1991, Dunning et al. 1995, Matthysen et al. 1995, Matthysen and Currie 1996). Some landscape elements may act as corridors and facilitate the movements of individuals of various species (Dunning et al. 1995, Haas 1995, Machtans et al. 1996, Rosenberg et al. 1997, St. Clair et al. 1998, Robichaud et al. 2002). However, little is known about the relative permeability of various habitat types to movements (but see Rosenberg et al. 1997). Why certain habitat types are relatively impermeable to movements is open to speculation, but a likely explanation is that species may lack the biological repertoire to bridge gaps of inhospitable habitat (Saunders et al. 1991) and use search tactics or rules inappropriate for these novel landscapes (Lima and Zollner 1996). Furthermore, reluctance to venture in certain habitat types may reflect decision-making by individuals perceiving an increased risk of predation due to insufficient or inadequate protective cover (Lima and Dill 1990, Rodriguez et al. 2001).

When moving through the landscape and encountering edges, forest birds might be more inclined to move across familiar habitats such as regenerating clearcuts than to venture into habitat types with contrasting structures such as agricultural fields (Sieving et al. 1996) or recent clearcuts (Stouffer and Bierregard 1995). Because clearcuts regenerate into their ''original'' state, they gradually become more permeable to forest bird movements (Robichaud et al. 2002). Hence, for forest songbirds and other species, the configuration of habitat mosaics and the relative permeability of habitat types will influence movement rates and trajectories of individuals and, hence, the degree of connectivity of the landscape. Hereafter, the combined effects of the amount, configuration, and resistance of habitats on observed bird movements will be referred to as landscape permeability. Permeability is synonymous to functional connectivity, except that it refers to the medium through which individuals are moving rather than to the behavioural response of the focal organism to this medium.

Little information is available on the extent and trajectory of dispersal movements for most species (Wiens 1996), especially long-distance migratory birds. Until technology allows us to track the movements of small songbird species over a full migratory cycle, we will have to rely upon alternative approaches to investigate their large-scale movements and their response to landscape structure. We view experimental translocations (Desrochers et al. 1999) as a promising alternative. Homing abilities of birds have been well documented, especially for the homing pigeon (*Columba livia*) (reviewed by Able 1995). Homing to territories following displacement has also been demonstrated in a few migratory species such as the wood thrush (*Hylocichla mustelina*) (Able et al. 1984) and the collared flycatcher (*Ficedula albicollis*) (Pärt 1995).

In this study, we used experimental translocations to compare the movements of a habitat specialist, the ovenbird (*Seiurus aurocapillus*), and a habitat generalist, the white-throated sparrow (*Zonotrichia albicollis*), in three contrasting types of forest landscapes in the boreal mixedwood zone of western Canada. These were: (1) a landscape fragmented by agriculture, (2) a landscape fragmented by forestry, and (3) a naturally patchy landscape. We compared the probability and time of return of individuals to their territory among landscape types to determine whether they differed in their permeability to movements. Based on their respective life history characteristics (see Methods), we predict that the ovenbird will show a greater sensitivity to landscape type and structure than the white-throated sparrow. In fact, we predict that the ovenbird will move more rapidly and efficiently in more forested landscapes whereas the white-throated sparrow will show no difference in its movement behaviour among the three forest landscape types.

Other factors may influence between-year site fidelity in adult birds and thus, potentially, their tendency to return to their territory after being displaced experimentally. Site fidelity has been shown to vary according to the age of individuals (Greenwood and Harvey 1982, Payne and Payne 1993, Pärt 1995, Holmes et al. 1996, Morton 1997), their pairing status (Pärt and Gustafsson 1989, Pärt 1994), their reproductive success (Holmes et al. 1996, Haas 1998), and the quality of their territory (Pärt 1994, Holmes et al. 1996). Moreover, older individuals tend to occupy higher quality sites, resulting in age-specific patterns in habitat distribution (Sherry and Holmes 1989, Holmes et al. 1996, Hasselquist 1998). Thus, we examined the influence of habitat characteristics at the capture site, physical characteristics and, to some extent, age and pairing status of individuals on movement patterns.

Methods

Study area

This study was conducted in the summers of 1998 and 1999 in the boreal mixedwood forest of north-central Alberta, Canada. Experiments were conducted in three

different forest landscape types: (1) a landscape fragmented by agriculture located west of Meanook (54°35′ N, 113°26′ W), (2) a landscape fragmented by timber harvesting located west of Calling Lake (55°27′ N, 113°67′ W) and (3) a naturally patchy landscape located north of Owl River (55°01′ N, 111°89′ W) (Fig. 1).

The landscape fragmented by agriculture covered approximately 5000 ha, with 30% forest scattered in small fragments surrounded by cropland and pastures. The majority of fragments were composed of mature to old forest dominated by trembling aspen (*Populus tremuloides*) or balsam poplar (*P. balsamifera*) with scattered white spruce (*Picea glauca*). In wet areas, black spruce (*Picea mariana*) and shrubs (*Alnus tenuifolia*, *A. crispa*, *Salix* spp.) tended to dominate. The harvested landscape covered 2000 ha, 75% of which was comprised of mature to old forest. Open areas consisted mainly (>95%) of clearcuts harvested in 1994 in a checkerboard pattern. Sixty percent of forest stands were dominated by trembling aspen. Coniferous stands were dominated by white spruce (18%), jack pine (*Pinus banksiana*) (13%), larch (*Larix laricina*) and black spruce (9%, combined). The naturally patchy landscape covered approximately 1400 ha, 80% of which was mature forest. Open areas consisted of bogs, wet shrubby areas, and clearcuts, but the latter were located mainly at the periphery of the study area. Trembling aspen dominated 78% of stands, followed by black spruce (11%) and other coniferous species (mainly larch and white spruce, 11%).

A second naturally patchy landscape was added in 1999. It was located 5 km north of the harvested landscape (55°29′ N–113°63′ W) and encompassed an area of 1500 ha, 90% of which was forested. The remaining 10% was composed of natural openings such as bogs and wet shrubby areas. Trembling aspen dominated 62% of forest stands, followed by black spruce (22%), white spruce (11%), and other coniferous species (5%).

Target species

We selected two target species for this study: (1) the ovenbird, and (2) the white-throated sparrow. These species are relatively abundant in the study area, they are relatively easy to detect and capture, but they differ in their habitat preferences. The ovenbird, a Neotropical migrant, is a habitat specialist with a strong affinity for closed canopy deciduous-dominated forest stands. It has been shown to be sensitive to habitat fragmentation throughout its breeding range (Van Horn and Donovan 1994). In Alberta, the ovenbird reaches its highest densities in mature aspen-dominated forest stands, but it is also relatively frequent in younger and older seral stages (Westworth and Telfer 1993, Schieck et al. 1995). The white-throated sparrow, a temperate migrant, is a generalist breeding in a variety of habitats ranging from regenerating clearcuts to mature forest with openings and dense low vegetation (Falls and Kopachena 1994). In Alberta, this species reaches its highest densities in open forest stands of various ages (Westworth and Telfer 1993, Schieck et al. 1995). It does not appear to be negatively affected by timber harvesting (Schmiegelow et al. 1997) and actually reaches high densities in recent clearcuts (Westworth and Telfer 1993). In forests fragmented by agriculture, the white-throated sparrow mainly occupies fragment edges with a dense shrub layer (Villard et al. 1999).
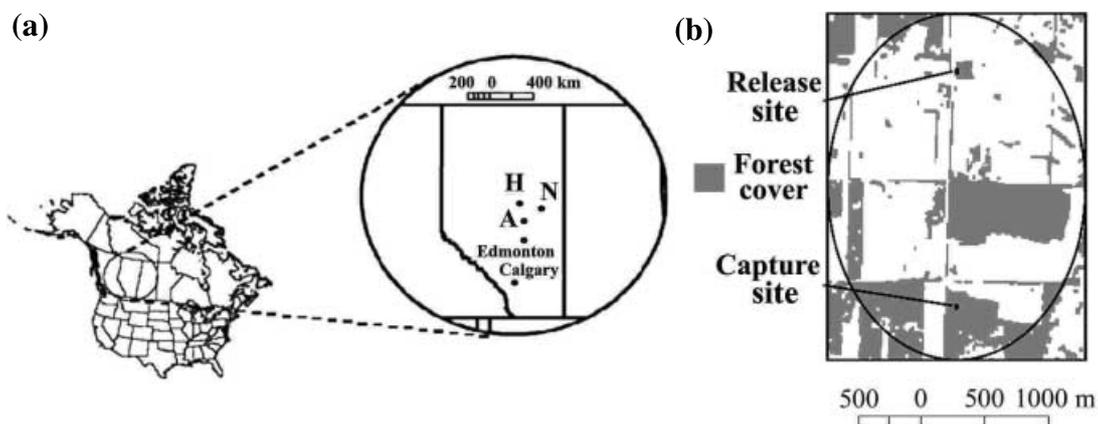

Fig. 1. (a) Location of the three forest landscape types where experimental translocations were performed: agricultural (A), harvested (H) and naturally patchy (N). (b) Landscape section corresponding to a single translocation. For each translocation, we drew an ellipse whose foci were the capture and release points and quantified landscape structure within the smallest rectangle encompassing this ellipse.

Experimental translocations

Within each landscape type, we selected sites for experimental translocations using 1:40 000 aerial photographs and 1:15 000 forest cover maps. For each translocation, we drew an ellipse whose foci were the potential points of capture and release. The ellipses had an arbitrary eccentricity value of 0.67 (Fig. 1). Each ellipse represented a translocation scenario, i.e. the area through which a displaced individual was likely to return. We released birds in forest fragments of at least 1 ha (the majority were larger) that were characterized by relatively mature aspen forest. Release sites were ground truthed ahead of time to ensure that vegetation met those criteria. Furthermore, we selected translocation scenarios whose corresponding ellipses mainly comprised mixedwood forest and man-made openings (i.e. agricultural fields or clearcuts) to reduce the potential influence of other land cover types on the outcome of translocations.

Most birds had a unique combination of capture and release sites. Of the 84 ovenbirds we translocated, we used the same translocation scenario for two different individuals in the agricultural landscape, whereas this occurred for three pairs of birds in the naturally patchy landscape. Out of these four pairs of birds, only one had the same probability and time of return in 24 h. Hence, it seems unlikely that repeating the same translocation scenario biases the outcome of translocations.

Translocations were performed between late-May and late-June each year. We determined the timing of translocations according to the breeding phenology of each species, i.e. from the time when males were strongly attached to their territory until young started to fledge. Only males were displaced because (1) they are easier to detect and capture and (2) their temporary absence is unlikely to cause reproductive failures. The presence of territorial males was determined a few days prior to their capture. We captured males in the early morning using mist nets, decoys (plastic and wooden painted models), pre-recorded songs/calls of conspecifics, or playbacks of songs of neighbouring males. Once an individual was captured, its sex was confirmed (cloacal protuberance) and we measured its weight and unflattened wing length. In 1999, we used plumage characteristics to age individuals as second year (SY) or after second year (ASY) following Pyle (1997). However, individuals with intermediate plumage characteristics are frequent and, thus, this technique might not be entirely reliable (Pyle 1997).

Each individual was banded with a numbered metal band and a unique combination of colour plastic bands. We then placed individuals in cloth bags which we inserted into a padded soundproof box to avoid any injuries and reduce stress while moving them to the release locations. We released individuals 1.5 to 2.7 km (median: 2.0 km) away from the site of their capture. These distances exceed those reported for breeding dispersal (Payne and Payne 1993, Morton 1997) and, consequently, we expected to detect effects of landscape structure on movements at this scale. Release sites were reached using a truck (in the agricultural landscape) or an all-terrain vehicle (in the other two forest landscape types). We drove all-terrain vehicles as slowly as possible to further reduce stress on birds. We reached release sites in approximately 15–40 minutes.

We translocated 1–3 birds every morning. Upon the release of translocated individuals, an observer returned to each capture site and played songs/calls for a total of 5 minutes every hour for the following 4 h. We examined the legs of every individual responding in the vicinity of the capture site in an attempt to locate the returning male. For individuals not returning within the initial 4 h, we conducted surveys the next mornings for a maximum of 48 h after their translocation. In 1998, we also returned to capture sites in the evenings to obtain data on returns every 12 h for 60 h. However, the detectability of individuals was lower in the evenings and only 6.6% of returning individuals (5 out of 76 birds translocated in 1998) were detected during these visits. Thus, we decided to restrict survey periods to the morning in 1999 (i.e. 4, 24 and 48 h after each translocation). In 1999, we also returned to territories 168 h after each translocation (for those that were unoccupied after 48 h) but no new returning birds were recorded. Over the two years of the study, 97% of returning birds (both species combined) were detected in the first 48 h.

Quantification of landscape structure

We mapped all study landscapes using ArcView GIS 3.1 (ESRI 1996). We obtained forest inventory maps from Alberta-Pacific Forest Industries and Weyerhaeuser Canada Ltd for the harvested and naturally patchy landscapes. These maps were based on the interpretation of 1:15 000 aerial photographs. For the agricultural landscape, we digitized 1:40 000 aerial photographs. The digitized images were then simplified using a supervised classification (ArcView Image Analysis 1.0, ERDAS 1998). Each image was classified as either (1) forest or (2) other land cover types. Forest cover consisted of forest stands ranging in age from young to mature/old. In the agricultural landscape type, this category also included hedgerows. Habitat types that resulted from human disturbance (e.g. fields, clearcuts) and natural openings (mainly wet shrubby areas, bogs) were classified in the other cover types category.

For the agricultural landscape, the classified map was compared and corrected using topographical maps that were ground-truthed during the field season. The map

Table 1. Meaning of variable codes.

COVER (%)	Proportion of woodland in the landscape section considered
EDGEDENS (m/ha)	Total length of edge between woodland and other cover types in the landscape section
LANDSCAPE	Type of forest landscape (AGRI = agricultural; HARVEST = harvested, NATURAL = naturally patchy)
MNN (m)	Mean distance between nearest-neighbour forest fragments in the landscape section
NFRAGMENTS	Number of forest fragments in the landscape section

was then converted to 1:15 000 grid maps to obtain the same resolution as that of the forest inventory maps for the other two landscape types. This was done to avoid potential problems associated with measuring metrics over different spatial scales (Haines-Young and Chopping 1996, but see Wickham and Riitters 1995). For each translocation performed, we characterized landscape structure in the smallest rectangle encompassing the corresponding ellipse (landscape section, Fig. 1). We used Fragstats 2.0 (McGarigal and Marks 1995) to measure the following metrics: forest cover (COVER), number of fragments (NFRAGMENTS), mean nearest-neighbour distance (MNN), and edge density (EDGEDENS) (see Table 1 for details). These metrics were selected because they reflect different aspects of landscape structure, that is, landscape composition, patch density, edge and interspersion metrics respectively (McGarigal and Marks 1995).

Statistical analyses

We used logistic regression models to assess the influence of independent variables on the probability of return of individual birds. We used Cox proportional hazard regression models (Parmar and Machin 1995) to examine the effects of the same variables on the time required by individuals to return to their territories. Because we were not always able to search for returning individuals in all capture sites at 4, 24, and 48 h after translocation, we used return/no return in 24 h as the dependent variable for logistic regressions. The loss of information is small because 82% of all returning birds (species combined) had been detected by 24 h. The time of return measured over 48 h was used as the response variable in Cox regressions since this method is designed for analysing failure-time data. In our case, a "failure" represented an individual returning to its territory. Individuals for which observations were stopped before the 48 h census period were treated as censored cases (Parmar and Machin 1995).

Our initial set of independent variables was the same for both statistical analyses. For all metrics, mean values differed significantly among landscape types (one-way ANOVA, $P < 0.001$; Table 2), except for MNN, which did not differ significantly between the harvested and naturally patchy landscapes (Tamhane's $T2$ multiple comparisons test, $P > 0.10$). As reported in other studies (Gustafson and Parker 1992, Hargis et al. 1998, Villard et al. 1999), landscape metrics were intercorrelated. MNN, EDGEDENS and NFRAGMENTS were all significantly negatively correlated with COVER when fitting linear or quadratic regressions (Table 3). Since there were significant differences in structure

Table 2. Mean values ($\pm$ SD) of forest cover and configuration metrics of all rectangular landscape sections combined for each forest landscape type. Ranges are shown in parentheses.

	Landscape type		
	Agricultural (n = 52)	Harvested (n = 56)	Naturally patchy (n = 40)
COVER (%)	30.6 ± 3.6 (22.4–42.2)	63.9 ± 4.8 (55.5–72.2)	90.3 ± 5.0 (82.3–98.0)
NFRAGMENTS	63.1 ± 17.1 (32.0–93.0)	14.6 ± 1.5 (12.0–19.0)	5.8 ± 2.7 (2.0–10.0)
MNN (m)	51.0 ± 5.3 (40.1–62.4)	31.3 ± 3.1 (24.6–43.9)	30.4 ± 9.0 (15.0–42.8)
EDGEDENS (m/ha)	82.3 ± 6.5 (66.9–100.4)	97.9 ± 9.1 (78.5–115.7)	43.8 ± 8.8 (24.6–53.3)

Table 3. Relationships between forest cover and other landscape metrics quantified in 148 rectangular landscape sections corresponding to experimental translocations. COVER^2 indicates a quadratic regression.

Variable	Parameter estimate		Intercept	R^2	P
	COVER	COVER^2			
log(NFRAGMENTS)	−0.02		2.31	0.93	<0.001
MNN	−1.36	0.01	84.13	0.71	<0.001
EDGEDENS	−4.01	−0.04	−2.84	0.91	<0.001

among landscape types, and landscape metrics were significantly intercorrelated, we used landscape type (LANDSCAPE) as a surrogate for all landscape metrics. In other words, LANDSCAPE was used as a variable to determine the overall effect of landscape type, which encapsulates the effects of (1) matrix type and (2) proportion and (3) configuration of forest in the landscape.

To account for the potential effects of variations in the body condition and physical characteristics of translocated individuals, we included a variable termed flight cost. We estimated flight metabolism (i.e. energy costs) based on the equation developed by Castro and Myers (1988), which takes into account the aerodynamic characteristics of individuals:

$$M = 2.23 \times W^{1.407} \times L^{-1.381}$$

where M is the flight metabolism (kJ/h), W represents the bird's weight (g), and L is wing length (cm). This equation thus assumes that the energy spent returning to the territory increases with body weight and decreases with wing length. Also, we included translocation distance to assess its effect on the probability and time of return of individuals because there was some variability around our mean translocation distance (2044 ± 274 m). We pooled both years of data for all of these variables. We also included date, year, and their interaction into the models to determine their effect on the outcome of translocations.

To assess the effect of age, we performed separate logistic and Cox regressions for individuals translocated in 1999 in the harvested landscape. We determined whether older males (ASY) had a higher probability to return and shorter return times than SY males. We restricted this analysis to the harvested landscape because most translocations were performed there in 1999.

Model fitting

Our objective was to select the most parsimonious models to predict the probability of return of each target species. First, we computed univariate models using the following independent variables: landscape type, translocation distance, flight cost, date, year, date × year. Significance was assessed using the likelihood ratio test (Hosmer and Lemeshow 1989). At this stage, we used a significance level of $\alpha = 0.10$. For categorical variables (i.e. landscape type, age), we also used the significance of the Wald statistic to assess whether individual categories of the variable were significant. We then built hierarchical models by entering the most significant variables first, and each of the other variables selected, using the likelihood ratio test to assess the significance of the contribution of each

new variable entered into the model. At this stage, we used an α level of 0.05. We assessed the goodness of fit of final models using the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 1989).

We followed the same procedure to select variables to be entered in the Cox regression models. We tested the significance of the final models using the likelihood ratio test (Parmar and Machin 1995). The assumption of proportional hazards was met (Parmar and Machin 1995). For both statistical approaches, we used an indicator type contrast for categorical variables (i.e. dummy coding, Norusis 1999). All analyses were performed using SPSS 10.0 (SPSS 1999).

Assessment of habitat quality and pairing status

To assess the relative quality of the territory held by each captured male, we sampled the vegetation in 40-m radius circles centred on capture sites. The area sampled (0.5 ha) is assumed to be representative of the territory since the territory sizes of our target species average approximately 1 ha (Falls and Kopachena 1994, Van Horn and Donovan 1994). Using standard methods, we measured the species composition, stem density and basal area of saplings (diameter at breast height – dbh ≤ 2 cm), poles (height > 1 m; dbh $= 2-8$ cm) and trees (dbh > 8 cm). We also estimated percent ground and canopy cover, as well as leaf litter depth. We used a stepwise discriminant analysis (McGarigal et al. 2000) to compare habitat characteristics between capture sites of returning and non-returning individuals (after 24 h). For the ovenbird, there were no significant differences in habitat between capture sites of returning and non-returning individuals ($P > 0.10$). For the white-throated sparrow, one canonical function was significant for the agricultural landscape (Wilk's $\lambda = 0.63$, $\chi^2 = 8.18$, df $= 1$, $P = 0.004$), but it only included leaf litter depth. This may reflect the greater variability in leaf litter depth in this landscape type ($\chi^2 = 3.9 \pm 1.9$ cm) compared to the harvested ($\chi^2 = 5.0 \pm 0.9$ cm) and naturally patchy landscapes ($\chi^2 = 5.3 \pm 1.4$ cm). Based on these results, we concluded that territory quality was unlikely to have a major influence on the probability of return of males of either target species in this study.

A more subtle indicator of territory quality would have been the pairing status of translocated males (Pärt and Gustafsson 1989, Pärt 1994). Owing to time constraints, we were only able to classify 11 ovenbirds and 12 white-throated sparrows as being paired, based on field observations (copulation observed, male and female caught in the net simultaneously, nest found near the capture site). The proportion of individuals returning in 48 h did not differ significantly between males classified as paired and those whose pairing status was unknown (normal approximation of chi-square test, $P > 0.10$). In spite of the limitations of our classifica-
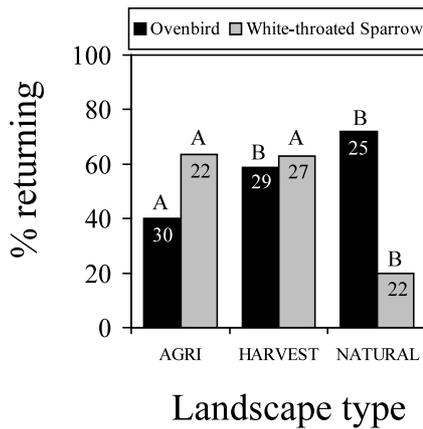
Fig. 2. Probability of return of ovenbirds and white-throated sparrows to their territory 24 h after translocation in the agricultural (AGRI), harvested (HARVEST) and naturally patchy (NATURAL) landscape types. Shared letters indicate no significant difference among landscape types for each species separately, according to Tukey multiple comparisons. Sample size (number of translocations performed) is shown in each bar.

tion, this suggests that pairing status did not have a major influence on the probability of return of translocated males. Based on these results, we did not include pairing status in the regression models.

Results

Probability and time of return

Over the two years of study, we captured and translocated 84 ovenbirds and 64 white-throated sparrows. As expected, the probability of return of ovenbirds after 24 h was lowest in the agricultural landscape and highest in the naturally patchy landscape (Fig. 2). The probability of return was lower in the harvested landscape than in the naturally patchy landscape, but the difference was not significant (Fig. 2). Ovenbirds returned significantly faster to their territory in the naturally patchy and harvested landscapes than in the agricultural landscape after the 4 and 24 h census periods (Fig. 3). However, after 48 h, only the naturally patchy landscape had a significantly greater cumulative proportion of returning individuals (Fig. 3).

The proportion of white-throated sparrows returning in 24 h was significantly lower in the naturally patchy landscape, but it was similar in the agricultural and harvested landscapes (Fig. 2). The latter two landscape types had similar cumulative proportions of returning individuals except in the initial 4 h, when a significantly greater proportion of individuals had returned to their territory in the harvested landscape (Fig. 3). The cumulative proportion of returning individuals was significantly lower in the naturally patchy landscape than in

the other two landscape types except for the initial 4 h, when it was similar to that observed in the agricultural landscape (Fig. 3).

Predictors of the probability and time of return

Ovenbird

When comparing all three landscapes types, results were consistent whether we used the probability or time of return as dependent variables. For the ovenbird, landscape type was the only significant predictor of the probability and time of return (Table 4 and 5). Ovenbirds had a significantly lower probability and longer
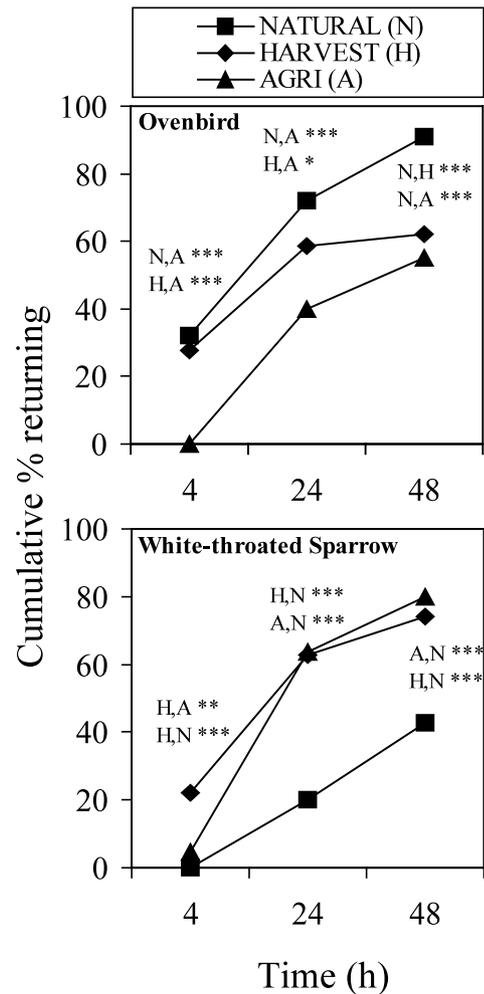

Fig. 3. Cumulative proportion of ovenbirds and white-throated sparrows returning to their territory as a function of time after translocation in three landscape types. Letters indicate the landscape types between which a significant difference in cumulative proportions was detected using a Tukey multiple comparison procedure (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). (Sample sizes for ovenbird/white-throated sparrow: AGRI, n = 30/22; HARVEST, n = 29/27; NATURAL, n = 25/15.)

Table 4. Logistic regression models predicting the probability of return after 24 h of each target species in agricultural (A), harvested (H), and naturally patchy landscapes (N), as a function of landscape type (LANDSCAPE).

	Ovenbird			White-throated sparrow			
Covariates	G [a]	P	Effect[b]	Covariates	G	P	Effect
All landscapes types combined (n = 84)				All landscapes types combined (n = 64)			
LANDSCAPE	5.89	0.05		LANDSCAPE	9.03	0.01	
A	5.40[c]	0.02	N > A	A		0.01	A > N
H	1.04	0.31		H		0.01	H > N
Agricultural vs natural (n = 55)				Agricultural vs natural (n = 37)			
LANDSCAPE	5.76	0.02	N > A	LANDSCAPE	7.20	0.01	A > N
				Harvested vs natural (n = 42)			
				LANDSCAPE	7.52	0.01	H > N

[a] $-2(LL_{\text{initial model}} - LL_{\text{model with covariate}})$
[b] Direction of effect. Landscape types where the probability of return is higher are indicated.
[c] Wald statistics and associated P values.

Table 5. Cox regression models predicting the time of return (max.: 48 h) for each target species in agricultural (A), harvested (H), and naturally patchy landscapes (N), as a function of forest landscape type (LANDSCAPE).

	Ovenbird			White-throated sparrow			
Covariates	G [a]	P	Effect[b]	Covariates	G	P	Effect
All landscapes types combined (n = 84)				All landscapes types combined (n = 64)			
LANDSCAPE	5.35	0.07		LANDSCAPE	4.99	0.08	
A	5.31	0.03	N < A	A	2.98	0.08	A < N
H	1.45	0.23		H	4.01	0.04	H < N
Agricultural vs natural (n = 55)				Agricultural vs natural (n = 37)			
LANDSCAPE	6.28	0.01	N < A	LANDSCAPE	3.69	0.06	A < N
				Harvested vs natural (n = 42)			
				LANDSCAPE	4.48	0.03	N < H

[a] See comments under Table 4.
[b] Direction of effect. Landscape types where return time is shorter are indicated.

times of return in the agricultural landscape than in the naturally patchy landscape (Table 4 and 5). When restricting the analysis to the agricultural and naturally patchy landscapes, landscape type was again the only significant predictor of the probability and time of return (Table 4 and 5). Individuals translocated in the agricultural landscape had a significantly lower probability to return and took significantly longer to return than those translocated in the naturally patchy landscape. As expected, a logistic regression model with forest cover (COVER) yielded similar predictions to those of the model with landscape type (Fig. 4). The probability of return of ovenbirds within 24 h increased significantly with increasing forest cover in the landscape ($G = 5.73$, df = 1, $P = 0.02$).

Neither translocation distance, date, year and their interaction, nor flight cost had a significant effect on the probability or time of return ($P > 0.10$). The age of 29 ovenbirds translocated in the harvested landscape also did not influence their probability of return ($G = 0.01$, df = 1, $P = 0.91$) nor their time of return ($G = 0.07$, df = 1, $P = 0.88$).

White-throated sparrow
Landscape type was the only significant predictor of the probability and time of return of white-throated sparrows (Table 4 and 5). White-throated sparrows were more successful and faster to return to their territory in both the agricultural and harvested landscapes (Table 4 and 5). When restricting the analysis to the harvested and naturally patchy landscapes, the effect of landscape type also was significant for both dependent variables (Table 4 and 5). When restricting the analysis to the agricultural and naturally patchy landscapes, landscape type had a significant effect on the probability of return (Table 4), but its effect on the time of return was only marginally significant (Table 5). Overall, the probability of return was significantly higher and the time of return significantly shorter in the agricultural and harvested landscapes than in the naturally patchy landscape (Table 4 and 5). In contrast with the ovenbird, a logistic regression model with forest cover (COVER) predicted the probability of return in 24 h differently than the model with landscape type (Fig. 4). Landscape type predicted similar return probabilities for the agricul-

tural and harvested landscapes, whereas forest cover predicted a significant decrease in the probability of return in 24 h with increasing forest cover but in a more linear fashion ($G = 4.76$, df = 1, $P = 0.03$). However, as suspected, forest cover was not a significant predictor of the probability of return in 24 h when comparing the agricultural and harvested landscapes only.

As for the ovenbird, neither the translocation distance, date, year and their interaction, nor flight cost were significant predictors of the probability and time of return of white-throated sparrows ($P > 0.10$). The age of 26 white-throated sparrows translocated in the harvested landscape did not influence their probability of return ($G = 0.02$, df = 1, $P = 0.88$) nor their time of return ($G = 0.02$, df = 1, $P = 0.90$).

Discussion

For both species examined, landscape type was the most significant predictor of probability and time of return of individuals to their territories. However, the nature of the landscapes we studied did not allow us to identify specific causal factors underlying the effect of landscape type (e.g. matrix type, proportion or configuration of woodland). Heavily forested agricultural landscapes and landscapes highly deforested by timber harvesting were simply too rare in north-central Alberta (Gobeil, pers obs.). Nonetheless, our results reveal interesting differences in the response of a habitat specialist (ovenbird) and a habitat generalist (white-throated sparrow) to landscape structure. For the ovenbird, our prediction was supported: the agricultural landscape was the least permeable, followed by the harvested and naturally patchy landscapes. Contrary to our prediction, the white-throated sparrow was not indifferent to landscape type or structure: although two of the three landscape types were equally permeable. The naturally patchy landscape was significantly less permeable to sparrow movements. Permeability to ovenbird movements increased with forest cover in the landscape, whereas it decreased with forest cover for the white-throated sparrow. It should be noted that the probability of return of the sparrow did not decrease significantly with forest cover when the analysis was restricted to the agricultural and harvested landscapes.

Experimental studies using song/call playbacks suggest that adults of various forest bird species are reluctant to cross gaps in the forest (Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998) and tend to make detours through the forest (Desrochers and Hannon 1997) or along forested corridors (St. Clair et al. 1998) to reach their destination. In this study, translocations were performed over distances exceeding those reported for breeding dispersal in most passerines (Robichaud 2000). Our results indicate that translocated male ovenbirds returned more promptly to their territories in landscapes with greater forest cover, suggesting that this relationship may also hold for dispersing juveniles. Thus, in forest birds, functional connectivity might increase with the proportion of forest in the landscape, even for long-distance migratory species.

Bélisle et al. (2001) conducted a similar study in Québec, Canada. They compared the probability and time of return of three forest bird species, including the ovenbird, translocated in agricultural landscapes containing either less or more than 50% woodland. Forest
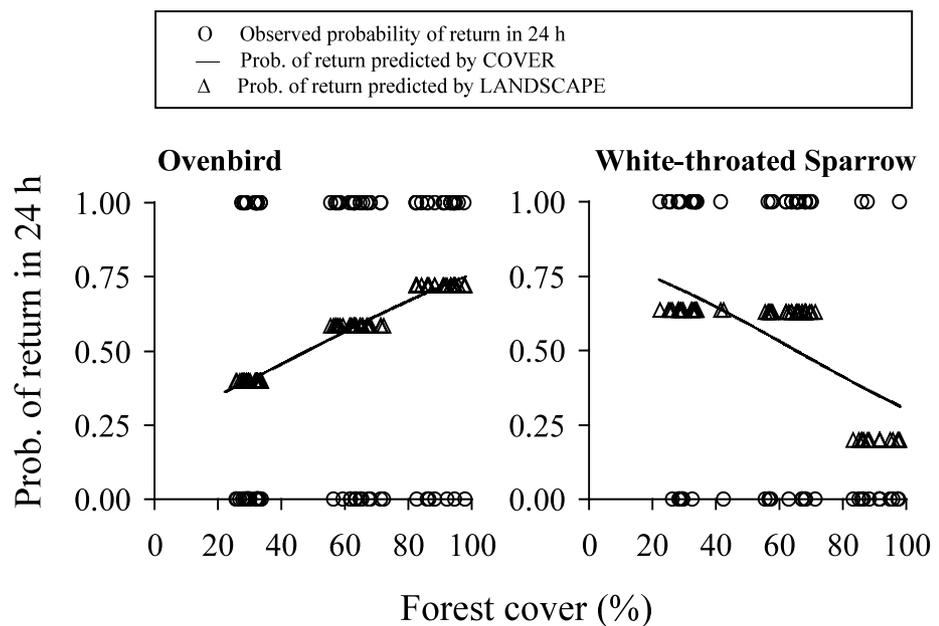

Fig. 4. Predicted probabilities of return in 24 h for translocated ovenbirds (n = 84) and white-throated sparrows (n = 64) according to logistic regression models with landscape type (LANDSCAPE) and forest cover (COVER) as the independent variable, respectively.

Legend:
O — Observed probability of return in 24 h
— Prob. of return predicted by COVER
Δ — Prob. of return predicted by LANDSCAPE

cover was the most significant predictor of the probability and time of return for their target species. They also examined the effect of landscape configuration using the residuals of forest configuration metrics after fitting forest cover. Only one of these metrics, the coefficient of variation in the mean nearest-neighbour distance among fragments, was significant. However, when entering configuration metrics rather than their residuals into models, all metrics were significant predictors of the probability of return. Based on these results, Bélisle et al. (2001) suggested that, in addition to forest cover, forest configuration probably influenced the probability and time of return of translocated birds. We obtained very similar results (Gobeil and Villard, unpubl.). However, owing to the contrasting structure of our three landscape types, we could not reliably distinguish the relative influence of forest cover and configuration. Nonetheless, results from this study and Bélisle et al.'s (2001) do indicate that ovenbird response to forest cover is consistent among widely-separated regions.

The positive influence of forest cover on ovenbird movements was expected. In contrast, we predicted that the white-throated sparrow would not respond to landscape type or structure. Indeed, movements of returning male sparrows were not influenced by landscape type when considering only the agricultural and harvested landscapes. However, sparrows were less likely to return or took longer to return in the naturally patchy landscape, when all three landscape types were considered. This may reflect our lower sample size in this landscape type. Alternatively, the lower permeability we observed in the naturally patchy landscape may reflect the fact that mature, closed-canopy forest tends to be suboptimal for reproduction of this species. Indeed, densities were lower in this landscape type (Gobeil, pers. obs.). In Alberta, this species reaches its highest densities in young and old forest stands (Westworth and Telfer 1993, Schieck et al. 1995), which are more likely to provide a dense shrub layer than mature, closed-canopy stands such as those found in large portions of our naturally patchy landscape. Thus, upon their release, some birds might have preferred to settle elsewhere, in more suitable habitat. Ideally, a map of suitable habitat for this species should have been based on the nature and structure of the shrub layer, but this was not possible with the land cover databases available.

To our knowledge, the only other study comparing movements of species with different degrees of habitat specialization is that of Haddad (1999). He compared the behaviours of three butterfly species in open habitat patches surrounded by forest and their use of corridors connecting these patches. Two habitat specialists "bounced back" into the open patch when encountering the forest edge and used corridors for interpatch movements more frequently than expected by chance.

In contrast, a habitat generalist species showed no response to forest edges and did not use corridors significantly more frequently than expected from random movements. It should be noted, however, that resources (host plants) were available to the generalist butterfly species inside the forest. We doubt that agricultural fields provided the resources (i.e. food/shelter) required by white-throated sparrows. Nonetheless, Haddad's (1999) study and ours do suggest that the functional connectivity of a given fragmented landscape is higher for habitat generalists than for habitat specialists.

Matrix permeability

In most fragmentation studies, including this one, landscapes are portrayed as binary mosaics of suitable and unsuitable habitats. However, the nature of the matrix is expected to influence the structural and functional connectivity of the landscape. By definition, matrix habitat is relatively inhospitable and may be perceived by moving organisms as relatively impermeable. Gap crossing experiments generally support this hypothesis for birds of mature forests (Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998). In this study, ovenbirds returned faster and more successfully in the harvested landscape than in the agricultural landscape, although the difference was not significant after 48 h. Unfortunately, we could not determine the relative influence of matrix type and forest cover on movement patterns owing to the fact that forest cover differed significantly among these two landscape types.

Experimental studies conducted on insect movement patterns indicate that some species (1) spend more time than expected by chance under vegetation cover when cover falls below a threshold range, and that (2) they move faster across inhospitable cover types (Wiens et al. 1997, Pither and Taylor 1998, McIntyre and Wiens 1999). As suggested by gap crossing experiments, ovenbirds might also prefer to move under forest cover for as long as possible before crossing openings. In the harvested landscape, the checkerboard harvest pattern may have allowed them to follow trajectories which avoid any gaps in forest cover. However, such a movement trajectory would have been longer than a more direct route across clearcuts. In the agricultural landscape, ovenbirds could not have travelled under forest cover over long distances given the small area of most fragments. However, it may have taken them time to decide to leave patches. Once outside the patch, they might have crossed open fields more rapidly owing to the lack of food and shelter and the potential threat of predation. This could explain why the cumulative proportion of returning individuals in the agricultural landscape was similar to that observed in the harvested landscape, but only after 48 h.

We must be careful when extrapolating results from translocation experiments into estimates of functional connectivity. For example, the fact that we obtained the

same cumulative proportion of returning ovenbirds in agricultural and harvested landscapes after 48 h does not mean that movement patterns of dispersing juveniles would be identical. Juvenile dispersers might be more reluctant to venture into open fields than into less contrasting habitats such as regenerating clearcuts.

In conclusion, this study indicates that for forest specialists such as the ovenbird, the permeability and, possibly, the functional connectivity of landscapes increase with the proportion of forest. Experimental translocations represent a useful technique to compare the permeability of different landscape types to the movements of organisms with strong site fidelity. Future studies could rely on this technique to further investigate the effect of matrix type and the relative influence of proportion vs configuration of suitable (or permeable!) habitat.

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