



Effects of forest regeneration on songbird movements in a managed forest landscape of Alberta, Canada

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Received 3 May 2001; accepted in revised form 19 October 2001

Key words: Alberta, Canada, Boreal mixedwood forest, Connectivity, Corridors, Dispersal, Forest songbirds, Forestry, Generalised additive models, Movements, Riparian buffer strip

Abstract

Recent studies have shown that barrier effects exist even in relatively vagile species such as forest songbirds. The objectives of this study were to determine whether a 560 × 100 m riparian buffer strip of mature forest was used as a movement corridor by forest songbirds and, if so, to what extent corridor effects persisted as woody vegetation regenerated in the adjacent clearcut. Over a 4-yr period, juvenile movement rates decreased in the riparian buffer strip and increased in the regenerating clearcut. Adult movement rates increased in the riparian buffer strip in the first year after logging, then gradually decreased, while still increasing in the regenerating clearcut. However, both juvenile and adult movement rates were higher in the buffer strip than in an undisturbed control site. Results suggest that most adults we captured held territories in the vicinity of the net lanes, and that most of the juveniles captured were dispersing away from their natal territory. Four years after harvest, juvenile movement rates were higher in the regenerating clearcut than in the riparian buffer strip, but several species had not yet been captured or detected in the regeneration. Our results suggest that the use of the riparian buffer strip as a movement corridor decreased with forest regeneration for both adults and juveniles. However, the buffer strip still acted as a movement corridor for the following species: Philadelphia and Red-eyed Vireos, Red-breasted Nuthatch, and Ovenbird.

Introduction

Dispersal is one of the key processes determining the probability of persistence of populations in fragmented landscapes (Merriam 1984, 1988, 1991; Hansson 1991; Wiens et al. 1993). Successful landscape-level conservation planning must therefore aim to maintain a high degree of connectivity (Taylor et al. 1993; Dunning et al. 1995; Sutcliffe and Thomas 1996; Thiebaut and Anderson 1997). Connectivity is defined as the “degree to which absolute isolation is prevented by landscape elements which allow organisms to move among patches” (Merriam 1991, p. 133). It does not simply refer to the degree of physical connection among habitat patches (i.e. connectedness) but specifically refers to the degree to which

populations exchange individuals through dispersal (Merriam 1984, 1991; Baudry and Merriam 1988). A high level of connectivity is considered essential to the long-term persistence of metapopulations in fragmented landscapes because it increases the probability of recolonisation after local extinction (Fahrig and Merriam 1985; Merriam and Saunders 1993).

Intuitively, the persistence of vagile organisms such as birds would not be expected to be influenced by the relative isolation of habitat patches. Bird population responses to habitat fragmentation, especially those of migratory species, are thus largely being studied with respect to other fragmentation effects such as area and edge effects (Freemark and Merriam 1986; Paton 1994; Burke and Nol 1998). However, physical isolation of habitat fragments may be accom-

panied by a decrease in connectivity if dispersal becomes hindered due to the distance among fragments or the inhospitability of the matrix (Lens and Dhondt 1994; Matthysen et al. 1995). Some indirect evidence suggests that this may be the case even in long-distance migrants (Askins et al. 1987; Robbins et al. 1989; Villard et al. 1995).

Natal and breeding dispersal of passerine birds are poorly documented, particularly in relation to patch isolation and matrix resistance in mosaic landscapes. This lack of information stems from the intrinsic difficulties involved in studying short-lived, vagile organisms whose dispersal movements can be complicated by migration. However, studies on migratory populations of White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) suggest that juvenile birds may select breeding territories for the following year during their postfledging dispersal phase (Morton et al. 1991; Morton 1997). If juveniles exhibit a certain behavioural reluctance to cross wide gaps in their habitat, it follows that their future distribution in a landscape will be influenced by the amount and configuration of suitable habitat. Adult response to habitat gaps may not be as strong as that of juveniles (Machtans et al. 1996), but they are still more likely to move along linking features when they are present in the landscape than to cross open spaces (Wegner and Merriam 1979; Johnson and Adkisson 1985; Haas 1995).

Although birds generally have the physical ability to move across inhospitable environments, there is evidence that habitat gaps can restrict forest bird movements both in the tropics (Terborgh and Weske 1969; Willis 1974; Karr 1982; Stouffer and Bierregaard 1995; Sieving et al. 1996) and in the temperate zone (Machtans et al. 1996; Desrochers and Hannon 1997; Rail et al. 1997; St. Clair et al. 1998). Metapopulation demography can, thus, be directly influenced by habitat configuration through its effects on connectivity. Movement corridors can be effective in maintaining or restoring connectivity in landscapes altered by human activities (Dunning et al. 1995; Machtans et al. 1996; Beier and Noss 1998). However, many studies on the possible use of landscape elements such as movement corridors have not convincingly established that the matrix was not used or rarely used for movements (see Beier and Noss (1998)).

Habitat loss and fragmentation had not been major concerns in the still relatively unbroken boreal mixed-wood forest of northern Alberta until recently. Ap-

proximately three-quarters of the province's forested lands have recently been leased to pulp and paper companies (Schmiegelow and Hannon 1993) and forest harvesting is gradually competing with fire as a significant agent of landscape change. In northern Alberta, harvest block size distribution is much narrower than that of fires: most fires tend to be smaller than 1 ha but the maximum fire sizes recorded are at least three orders of magnitude larger than harvest blocks (Johnson et al. 1998). The spatial pattern of fires is also much more complex than that of harvesting, although new harvest practices have changed from "wavy-edged" rectangular blocks distributed in a checkerboard pattern to harvest blocks dispersed over much larger areas (E. Dzus, Alberta-Pacific Forest Industries Inc., pers. com.). In Alberta, forestry companies are required by provincial regulations to leave a strip of vegetation along water bodies to act mainly as a buffer for water quality (Hornbeck et al. 1986; Barling and Moore 1994). As shown by Machtans et al. (1996), these buffer strips may play an additional role in managed forest landscapes by acting as movement corridors for some forest bird species.

In this study, we compared movement rates of forest birds (Appendix) in a riparian buffer strip composed of mature forest to those occurring in an adjacent regenerating clearcut. Results from the first three years of this study (Machtans et al. 1996) showed that riparian buffer strips could act as movement corridors for forest birds, at least for juveniles. We further tested the corridor function of this strip of forest by documenting movements over a 5-yr period to determine to what extent movement patterns of forest birds were influenced by the rapid regeneration of woody vegetation in the adjacent clearcut. To our knowledge, this is the first study documenting the effects of changes in the matrix on corridor use for movements.

We measured movement rates in a riparian buffer strip 1 yr before and in the 4 yrs after its creation by clearcutting of adjacent forest. These movement rates were compared to those measured in a control site (continuous lakeshore forest) and in the regenerating forest. We predicted that 1) after the initial increase in movement rates in the riparian buffer strip following clearcutting of adjacent forest, capture rates of forest birds would decrease as the clearcut regenerated. As some species stop considering the regenerating clearcut as inhospitable for movement or reproduction, we expected 2) an increase in movement rates over time in the regenerating clearcut. However, in the relatively short time window of this study, we

still predicted higher movement rates or in the riparian buffer strip than 3) in the adjacent clearcut or 4) in a control site where the adjacent forest was left undisturbed. Our time series also allowed us to examine the sequence with which certain species start using the forest regeneration for movement or reproduction and, in turn, which species require forested corridors over a longer period.

Methods

The study was conducted west of Calling Lake (55°15' N, 113°19' W), approximately 250 km north of Edmonton, Alberta, Canada, in the boreal mixed-wood forest region (Rowe 1972). Further details on the region encompassing the study area can be found in Schmiegelow et al. (1997). This study extends the time series of Machtans et al. (1996) at the "west buffer" site. Our treatment site consisted of a 560 m long by 100 m wide riparian buffer strip created by clearcutting of adjacent forest over at least a 200 m width from the buffer strip. The strip connected forest fragments of 10 and 40 ha (Figure 1). We monitored movements during the breeding and postfledging seasons (late May to mid-August) for 1 yr (1993) prior to and 4 yrs (1994–1997) after the creation of the riparian buffer strip. We installed two 100 m wide mist net lanes across the width of the riparian buffer strip. Nets were 2.6 m high. The pre-harvest year was used as a temporal control for movements in the buffer strip. In 1994, we also added mist net lanes in a continuous stretch of forest along the same lake edge to act as a spatial control (Figure 1). We visited each site every 10 days in the beginning of the season, and every 5 days starting in late June-early July, when juveniles were starting to leave their natal territory. We opened nets for 6 h starting in the first half-hour after dawn. More details on the specific layout of mist net lanes and on the mist netting protocol can be found in Machtans et al. (1996).

Machtans et al. (1996) conducted visual observations in the regenerating clearcut in the first and second years after harvest (1994 and 1995). They recorded all individuals flying across the regenerating clearcut at or below the height of our mist nets in a 100 m wide area adjacent to the riparian buffer strip (Machtans et al. 1996). In the third and fourth years after harvest (1996 and 1997), forest regeneration was high enough to allow the use of mist nets. We installed two 50 m mist net lanes in the regenerating

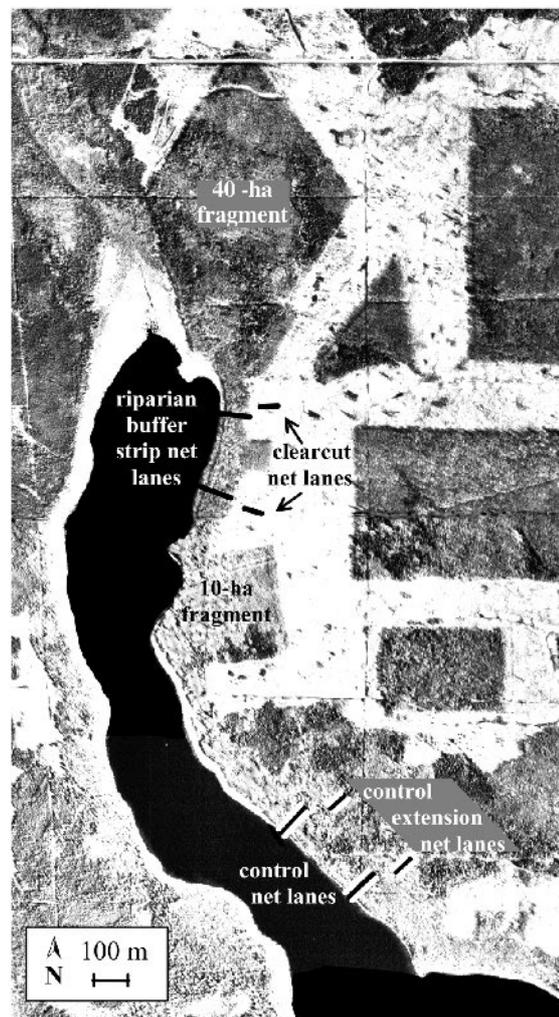


Figure 1. Aerial photograph of the study area, showing the location of net lanes in the riparian buffer strip, the regenerating clearcut and the control, and the layout of the forest fragments after experimental harvesting in the winter of 1993–94.

clearcut adjacent to the riparian buffer strip. We left a 50 m gap between the nets and the upland edge of the riparian buffer strip to ensure that the individuals we captured in the regenerating clearcut actually were moving outside the buffer strip, and not simply following its edge (Dickson 1982). We also added a 50 m net lane to each control lane in the same configuration and distance from the lake edge as in the regenerating clearcut (hereafter called control extensions). These 50 m net lanes were positioned perpendicular to the lake edge in both the control and the regenerating clearcut. Starting from the second year after harvest, we measured the height of the five nearest saplings every 5 m along two 100 m transects

running from the forest edge into the regenerating clearcut, for a total of 100 saplings/transect/yr. These data were collected in mid-summer, after the spring elongation phase of the saplings.

Data analysis

Adult and juvenile capture rates were analysed separately because adults and juveniles move for different reasons. Juvenile captures can include fledglings on their natal territory or dispersing juveniles. Adult captures may represent local movements for foraging or territory defence, off-territory explorations (Nolan 1978), breeding dispersal or movements by floaters. We restricted our analyses to the first captures of any individual in each year and site to ensure independence in our data and to limit the influence of local movements by territory holders on capture rates. Total netting hours differed slightly among years and sites due to the weather, although we repeated netting sessions or hours missed owing to bad weather whenever possible. To account for these differences, we standardised capture rates by dividing them by the actual total number of netting hours and expressing them as the number of new captures per 100 m of nets for the entire netting season (66 h at each site).

We mapped all territories in and around each site following the protocol described in Bibby et al. (1992) to account for variations in abundance of local territorial birds among years and sites and to control their potential effects on capture rates. We used local or regional territory densities obtained by spot mapping as explanatory variables in our analyses. Local territory density (LOCAL) is the total number of territories of each species per 10 ha in the site where the net lanes were located. Regional territory density (REGION) was calculated from a larger area: for the analyses of capture rates in the riparian buffer strip over the 1993–1997 period and in the regenerating clearcut, regional territory density was calculated based on territory maps from the riparian buffer strip and the two connected fragments (Figure 1). For comparisons of capture rates between the treatment and control sites, we calculated regional territory density over the riparian buffer strip, the two fragments and the control site.

We analysed corridor effects only on bird species present in the study area during the 5 years of the study which nest in mature or old boreal mixedwood forest. Species captured, but excluded based on this criterion, were Alder Flycatcher, Magnolia Warbler,

Northern Waterthrush, Common Yellowthroat, Wilson's Warbler, Clay-colored Sparrow, Le Conte's Sparrow, Nelson's Sharp-tailed Sparrow, Song Sparrow, Lincoln's Sparrow, Swamp Sparrow and Red-winged Blackbird (see Appendix for scientific names). Brown-headed Cowbird also was excluded because it does not hold territories. Cedar Waxwing was excluded because it cannot be reliably surveyed using spot mapping.

We used an alpha level of 0.10 to reduce the risk of making Type II errors (Peterman 1990; Smith 1995). We had sufficient data to test predictions 1 and 4 using generalised additive models (GAMs, see below). To test prediction 3, we used standardised capture rates but did not correct for territory densities because each comparison was made separately for each year. Prediction 2 could not be statistically tested owing to the different sampling methods used between the first and last two years, and because sample sizes were relatively small.

We used GAMs because they are not restricted to linear relationships between covariates, and can also indicate the effects of variables of interest (mainly year and site) adjusted for confounding variables (e.g., territory density). GAMs are a nonparametric extension of generalised linear models (GLMs), where the independent variables are not assumed to be linear, but rather the sum of unspecified smooth functions (Hastie and Tibshirani 1986, 1990). See e.g., Yee and Mitchell (1991); Tonteri (1994); Preisler et al. (1997); Fewster et al. (2000) and references therein for further explanation of their applicability in ecology.

We used a quasi-likelihood estimation to ensure that our data distribution (assumed to be a Poisson) was treated appropriately. Territory density was used as a covariate in the models. Two models were used, hereafter referred to as local or regional model, because local and regional territory densities were significantly correlated (Spearman's rank correlation, $r = 0.73$, $P < 0.001$) and therefore could not be used as explanatory variables in the same model. Final models were selected by starting with full models and iteratively subtracting non-significant variables. Interactions were examined using residuals. GLMs were used for this since GAMs do not permit these analyses directly (T. Hastie, pers. com.). However, sample sizes were too small to test several interactions using this method.

We constructed separate models to test predictions 1 and 4. For prediction 1, we used data from the ri-

Table 1. Standardized capture rates (new captures/100 m) for all species captured in each site and year. Territory densities (/10 ha) are only reported for species that were captured in the site(s) and year considered.

Site		1993		1994		1995		1996		1997	
		Adults	Juv.								
Buffer	<i>n</i> (spp.)	13	6	8	7	22	9	16	5	15	5
	Capture rate	24.9	3.8	17.9	10.2	47.7	8.2	37.7	7.6	32.0	5.0
	¹ LOCAL	30.0	10.0	32.9	12.1	50.7	15.0	55.7	34.3	65.7	16.4
	² REGION	17.9	8.9	18.2	12.5	25.2	9.6	30.2	17.3	32.9	12.3
	³ REGION	–	–	18.6	12.6	24.3	9.0	27.4	15.1	31.3	11.7
Control	<i>n</i> (spp.)	–	–	11	7	16	8	15	6	11	4
	Capture rate	–	–	14.8	4.3	22.1	6.1	19.9	4.1	12.0	5.0
	LOCAL	–	–	20.0	14.3	19.3	10.0	17.9	11.4	24.3	10.0
	³ REGION	–	–	19.0	15.9	22.3	11.1	26.6	16.4	17.6	12.6
Regen. clearcut	<i>n</i> (spp.)	–	–	–	–	–	–	8	5	8	7
	Capture rate	–	–	–	–	–	–	45.4	7.2	53.0	23.0
	LOCAL	–	–	–	–	–	–	33.0	4.0	29.0	27.0
	⁴ REGION	–	–	–	–	–	–	22.6	7.9	23.0	20.6
Control extension	<i>n</i> (spp.)	–	–	–	–	–	–	9	1	6	2
	Capture rate	–	–	–	–	–	–	14.2	1.0	13.0	3.0
	LOCAL	–	–	–	–	–	–	11.8	0.6	9.4	7.1
	⁵ REGION	–	–	–	–	–	–	16.8	0.1	13.8	8.8

¹Local density, i.e. density in the site considered.

²Regional density in the riparian buffer strip and the adjoining forest fragments

³Regional density in the riparian buffer strip, the fragments and the control site

⁴Regional density in the riparian buffer strip, the adjoining fragments and the regenerating clearcut

⁵Regional density in the riparian buffer strip, the fragments, the control site and the control extension area (Figure 1).

riparian buffer strip over the 5-year period; we tested the significance of year (YEAR) and we included species (SP) and LOCAL or REGION in the model to account for their confounding effects. For prediction 4, we used data from all four post-harvest years and tested for the significance of site (SITE) as a predictor of differences in capture rates. The covariates were YEAR, SP, and LOCAL or REGION. Eight different GAMs were thus computed: (1) temporal variation in capture rates in the treatment site and (2) spatial variation in capture rates between the treatment and control sites \times two age classes (juveniles vs. adults) \times two density variables (LOCAL vs. REGION) (Table 1).

Because juvenile captures in the riparian buffer strip were relatively low compared to other GAM data sets, we tested the sensitivity of GAMs to changes in the distribution of captures by randomly shifting a subset of captures among years for a given species. We randomly selected 5, 7, or 10 birds in the data set, representing respectively 7, 10 and 14% of

Table 2. Analysis of deviance table for the regional density model of adult capture rates of forest-nesting species in the riparian buffer strip in 1993–97. The selected model is $s(\text{REGION}) + s(\text{YEAR}) + \text{SP}$. The symbol $s()$ stands for smoothing spline and signifies that the variable has a non-linear effect.

Variable	Δ deviance	Δ d.f.	<i>F</i> -ratio	<i>P</i>
Smoothing of REGION ¹	2.341	3.015	2.700	0.058
$s(\text{REGION})$	9.679	4.015	8.385	<0.001
Smoothing of YEAR ¹	0.001	0.017	0.117	0.057
$s(\text{YEAR})$	5.740	3.979	5.017	0.002
SP	33.653	25.987	4.504	<0.001
Selected model	140.928	33.995	14.419	<0.001

¹This tests whether the non-linear (smoothed) form of the variable better fits the data than its linear form.

the 71 juveniles captured over the 5 years. Then, we applied the GAM that we had selected for the observed data set in each simulation. This procedure was repeated 10 times for each of the three subsets and we averaged the estimated effects for each year.

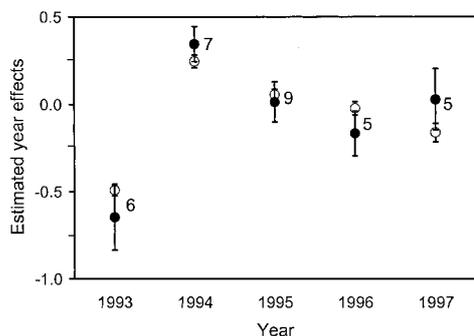


Figure 2. Estimated effects (± 1 SE) of each year on observed (closed circles) and simulated (open circles) capture rates of juveniles in the riparian buffer strip in 1993–97. The number of species included in the captures is shown for each year. Only the results of the random shifting of 14% of the captures are shown.

We then compared the results of these randomizations to those obtained with the actual data set (Figure 2). These results indicate that the GAM is robust to a moderate, randomized change in capture distribution: indeed, the trend in year effects is very similar to that obtained from the original data (Figure 2).

Results

Clearcut regeneration after harvest

Woody regeneration in the clearcut adjacent to the corridor was very rapid. Sapling height increased significantly every year between 1995 and 1997 (one-factor ANOVA; $F_{2,585} = 200.8$, $P < 0.001$; Scheffe post-hoc test, all $P < 0.001$). Mean sapling heights (\pm SE) were 78.51 (± 2.50) cm in 1995, 141.81 (± 3.64) cm in 1996, and 173.76 (± 4.05) cm in 1997. The woody regeneration was dominated by trembling aspen (*Populus tremuloides*, 90.5% of stems), with small proportions of paper birch (*Betula papyrifera*, 3.7%), balsam poplar (*P. balsamifera*, 3.0%) and willows (*Salix* spp., 2.0%). Sapling height did not vary significantly with distance from the forest edge in any of the three years (Pearson's correlation, $|r| < 0.09$, $n = 588$, $P = 0.230$).

Temporal changes in capture rates in the riparian buffer strip

Adults

We captured 327 adults of 27 species over the 5 yr period. Capture rates in the buffer strip varied over the 5-yr study. They dropped immediately after isola-

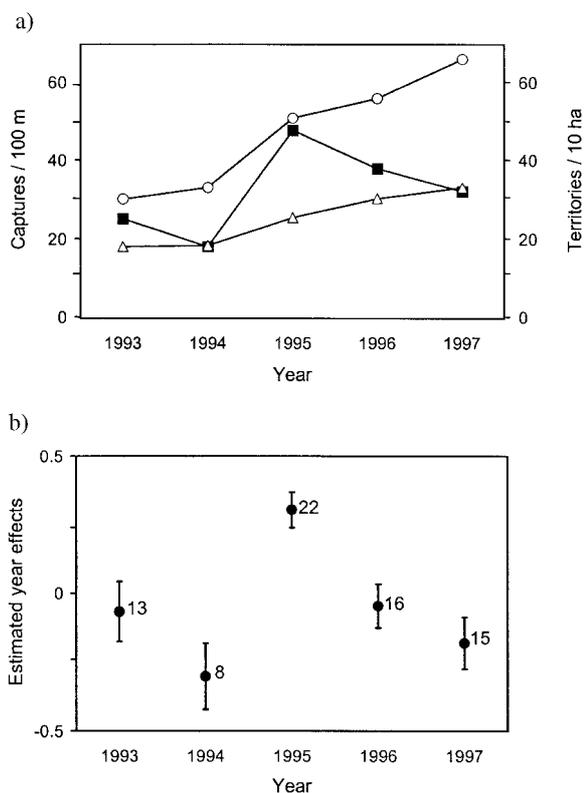


Figure 3. a) Temporal variation in standardised capture rates of adults in the riparian buffer strip (closed squares), with local (open circles) and regional (open triangles) territory density, b) estimated effects (± 1 SE) of year on capture rates in the GAM when regional territory density is considered. The number of species is indicated.

tion (1994), but then rebounded for the remaining 3 yrs, tapering off in each successive year of the study (Figure 3a). Standardised capture rates for all years are indicated in Table 1. The best fitting GAM is shown in Table 2.

Capture rates were significantly correlated with local and regional territory density (Spearman's rank correlation, $r \geq 0.64$, $n = 74$, $P < 0.001$). Hence, we used GAMs to determine whether capture rates differed among years independently of confounding factors. Using regional territory density as a covariate provided the best model fit (comparison with local territory density: analysis of deviance, $F_{3,90} = 4.86$, $P = 0.003$). The increase in captures in the second year after harvest was significant, as was the subsequent decline in the third and fourth years (Figure 3b).

The influence of territory density varied among models. Species with regional territory densities approximately >1.5 territories/10 ha were captured more frequently than expected, while species with 1 or fewer territories per 10 ha were captured less fre-

quently. Species with local territory density approximately lower than 2 or higher than 4 territories/10 ha were respectively captured less and more frequently than expected in the local model.

The most frequently captured species were Least Flycatcher, White-throated Sparrow, Ovenbird and Yellow-rumped Warbler. Some species were captured more frequently than expected from their territory densities. These included Least Flycatcher and White-throated Sparrow (both models), Ovenbird and Tennessee Warbler (local model), and Black-capped Chickadee (regional model). Red-eyed Vireos were captured less frequently than expected (both models), as were Connecticut Warblers (regional model).

Juveniles

We captured 71 juveniles of 15 species over the 5 yrs of the study in the buffer strip. Capture rates increased significantly after isolation of the buffer strip by harvesting (Figure 2). They remained elevated thereafter, with a decreasing trend. Our sensitivity analysis indicates that the trend in estimated year effects was robust in spite of the relatively small sample size (Figure 2).

Capture rates were significantly related to regional territory density (Spearman's rank correlation, $r = 0.36$, $n = 32$, $P = 0.04$), but they were not correlated with local territory density (Spearman's rank correlation, $r = 0.24$, $n = 32$, $P = 0.18$). Several species were caught in years when there were no territories of the corresponding species in the buffer strip. These were Dark-eyed Junco and Hermit Thrush (3 yrs), and Canada Warbler, Connecticut Warbler, Tennessee Warbler, Swainson's Thrush and Black-capped Chickadee (1 yr each).

Despite the significant correlation between regional territory density and capture rates, the GAM that best fitted the data did not include either local or regional territory density (Table 3). Capture rates thus varied much more according to species and years than as a function of density.

Adults vs. juveniles

When comparing the number of captures of adults and juveniles during the weeks when individuals of both age classes were captured, we found a significant difference (fewer juvenile captures) in 1995 only (Wilcoxon signed-ranks test, two-tailed, $Z = 2.12$, $P = 0.034$).

Table 3. Analysis of deviance table for juvenile captures of forest-nesting species in the riparian buffer strip in 1993–97. The selected model is $s(\text{YEAR}) + \text{SP}$. The symbol $s()$ stands for smoothing spline and signifies that the variable has a non-linear effect.

Variable	Δ deviance	Δ d.f.	F -ratio	P
Smoothing of YEAR ¹	< 0.001	0.020	0.040	0.070
$s(\text{YEAR})$	2.519	3.980	4.426	0.018
SP	14.801	14.000	7.394	< 0.001
Selected model	18.054	17.980	7.023	< 0.001

¹This tests whether the non-linear (smoothed) form of the variable better fits the data than its linear form.

Movements in the regenerating clearcut

Species captured

The regenerating clearcut was gradually colonised by new species over the four post-harvest years. The total number of forest-nesting species observed in the clearcut increased until the third and fourth year post-harvest, when it remained relatively stable (Table 4). In contrast, the number of species captured in the last two post-harvest years in the control extension net lanes actually decreased: nine species were captured in 1996 and six in 1997. Many of the species captured in the regenerating clearcut did not hold territories there: 64% (7/11 species) in 1996 (Least Flycatcher, Black-capped Chickadee, Hermit Thrush, Tennessee Warbler, Yellow-rumped Warbler, Connecticut Warbler, Western Tanager), and 50% (5/10) in 1997 (Yellow-bellied Sapsucker, Least Flycatcher, Swainson's Thrush, Yellow-rumped Warbler, Purple Finch). On the other hand, most of the species captured in the control extension net lanes held territories in the vicinity (78% of species in 1996 and 83% in 1997). Machtans et al. (1996) had also found an increase in the number of species using the regenerating clearcut based on direct observations over the first two years after harvest.

Adult capture rates

A total of 38 adults were captured in the regenerating clearcut in 1996 only (Figure 4), and another six (one Least Flycatcher, one Tennessee Warbler, two White-throated Sparrows and two Yellow-bellied Sapsuckers) were captured in both the riparian buffer strip and the regenerating clearcut. In 1997, 47 individuals were captured in the regeneration only (Figure 4), and seven also were captured both in the regenerating clearcut and in the riparian buffer strip. Capture rates increased substantially for Tennessee Warbler and, to

Table 4. Species observed in the regenerating clearcut at mist net height (\leq ca. 2.5 m), within 100 m of the riparian buffer strip (1994, 1995), or captured in mist nets in the clearcut (1996, 1997). The clearcut was created in the winter of 1993–94. See Appendix for scientific names.

Species	1994	1995	1996	1997
Dark-eyed Junco	•			
American Robin	•	•		
Hairy Woodpecker	•	•		
Yellow-bellied Sapsucker	•	•	•	•
White-throated Sparrow	•	•	•	•
Chipping Sparrow	•		•	•
Black-capped Chickadee		•	•	
Connecticut Warbler		•	•	
Least Flycatcher		•	•	•
Mourning Warbler		•	•	•
Hermit Thrush			•	
Western Tanager			•	
Tennessee Warbler			•	•
Yellow-rumped Warbler			•	•
Purple Finch				•
Swainson's Thrush				•
Yellow Warbler				•
Total number of species	6	8	11	10

a lesser extent, for Yellow Warbler between 1996 and 1997 in the regenerating clearcut (Figure 4). In comparison, there was no increase in captures in the control extension net lanes (13 versus 14 individuals in 1996 and 1997, respectively).

Juvenile capture rates

There was an overall increase in capture rates, from 7 captures in 1996 to 23 in 1997 (Figure 4). Tennessee Warbler, White-throated Sparrow and Mourning Warbler showed the greatest increase in capture rates in the regenerating clearcut (Figure 4). Over the same period, captures in control extensions were low: 1 and 3 juveniles were captured in 1996 and 1997, respectively.

Spatial variation in capture rates: regenerating clearcut vs. riparian buffer strip

Adults

Capture rates in the buffer strip were similar to those in the regenerating clearcut in both 1996 and 1997 (one-tailed Wilcoxon rank-sum tests on captures per mist netting period for all species combined; 1996: $Z = -0.92$, $P = 0.822$; 1997: $Z = -1.09$, $P = 0.863$).

Capture rates actually were higher in the regenerating clearcut in 1997, but not significantly so (two-tailed Wilcoxon rank-sum test, $Z = -1.03$, $P = 0.304$). The timing of captures throughout the season (relating to movement types) also was similar between the two habitat types (two-tailed Wilcoxon signed-ranks tests by year, $Z \leq -0.80$, $P \geq 0.28$).

The species composition of captures differed between the buffer strip and the regenerating clearcut. Several species captured in the buffer strip were never captured in the regenerating clearcut, while the opposite was not found. In 1996, a total of 16 species were captured in both areas combined. Half of these (8) were captured exclusively in the riparian buffer strip, whereas none were captured only in the regenerating clearcut (Figure 4). Species that had higher capture rates in the regenerating clearcut than in the riparian buffer strip were Mourning Warbler and White-throated Sparrow and, to a lesser extent, Western Tanager and Chipping Sparrow (Figure 4). In 1997, a total of 17 species were captured in both areas. Nine (53%) of these were unique to the riparian buffer strip, whereas only two (Mourning Warbler and Chipping Sparrow) were exclusive to the regenerating clearcut. Tennessee and Yellow Warblers and White-throated Sparrow had higher capture rates in the regenerating clearcut (Figure 4). In 1997, if we compare only the species captured in the riparian buffer strip, capture rates still were not significantly higher than in the regenerating clearcut (one-tailed Wilcoxon signed-ranks test, $Z = 0.94$, $P = 0.173$).

Juveniles

Juvenile capture rates did not differ between the regenerating clearcut and the riparian buffer strip. Capture rates per mist netting period were not significantly higher in the riparian buffer strip (1996: one-tailed t-test on $\log(x+1)$ -transformed data, $t = 0.17$, $n = 11$, $P = 0.434$; 1997: one-tailed Wilcoxon rank-sum test, $Z = -1.26$, $P = 0.895$). Similarly, capture rates per species were not significantly higher in the riparian buffer strip (one-tailed Wilcoxon signed-ranks tests; 1996: $Z = -0.35$, $P = 0.638$; 1997: $Z = -1.84$, $P = 0.967$; Figure 4). In fact, when using a two-tailed test, capture rates were higher in the regenerating clearcut than in the riparian buffer strip in 1997 ($Z = -1.74$, $P = 0.082$).

As for adults, the species composition of captures differed between the two habitat types. In 1996, only two out of eight species (Tennessee Warbler and Yellow-bellied Sapsucker) were captured both in the re-

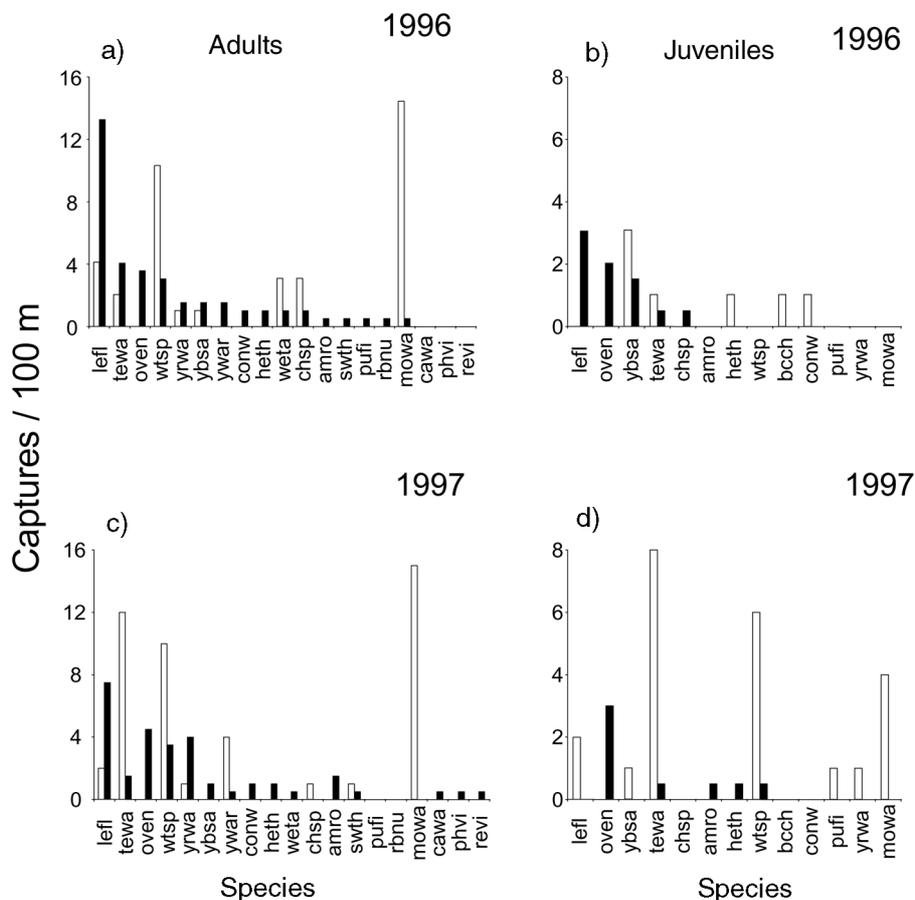


Figure 4. Capture rates per species in the regenerating clearcut (white) and the riparian buffer strip (black). Individuals that were captured in both sites are excluded. See Appendix for species codes. Note differing scales for a) and c) vs b) and d).

generating clearcut and the riparian buffer strip. Connecticut Warbler, Black-capped Chickadee and Hermit Thrush were captured exclusively in the regenerating clearcut (Figure 4). Again, in 1997 only two out of ten species (White-throated Sparrow and Tennessee Warbler) were captured in both habitat types, but in higher numbers in the regenerating clearcut. Yellow-bellied Sapsucker, Least Flycatcher, Mourning and Yellow-rumped warblers, and Purple Finch were only captured in the regenerating clearcut (Figure 4).

In 1996, the timing of juvenile captures (all species combined) did not differ between the riparian buffer strip and the regenerating clearcut (two-tailed paired t-test; $t = 0.20$, $n = 6$, $P = 0.852$). There was a peak in captures around the third week of July in both sites. However in 1997, capture rates were still relatively high in early August in the regenerating clearcut, while they decreased in the riparian buffer strip after a peak in mid-July (Wilcoxon signed-ranks test, two-tailed, $Z = -1.69$, $P = 0.092$).

Spatial variation in capture rates: riparian buffer strip vs. control

Adults

Over the four years of operation of mist nets in the control (1994–1997), we captured 142 adults of 23 species. There were more new captures in the riparian buffer strip than in the control site in all years after harvest (Table 1). However, as in the riparian buffer strip (see Temporal changes in capture rates in the riparian buffer strip), capture rates in the control site were correlated with both local and regional territory density (Spearman's rank correlation, $r \geq 0.48$, $n = 53$, $P < 0.001$). When taking into account local and regional territory density in GAMs, capture rates were still significantly higher in the riparian buffer strip than in the control site (Figure 5, Table 5).

The two models did not fit the data equally well. The fit was significantly better for the local density model (analysis of deviance, $F_{3,03} = 23.46$, $P <$

Table 5. Analysis of deviance table for the local territory density model of adult capture rates of forest-nesting species in the riparian buffer strip and the control in 1994–97. The selected model is $s(\text{LOCAL}) + s(\text{YEAR}) + \text{SITE} + \text{SP}$. The symbol $s()$ stands for smoothing spline and signifies that the variable has a non-linear effect

Variable	Δ deviance	Δ d.f.	F-ratio	P
Smoothing of LOCAL ¹	3.328	3.031	3.162	0.029
$s(\text{LOCAL})$	32.892	4.031	23.499	<0.001
Smoothing of YEAR ¹	0.006	0.009	1.770	0.019
$s(\text{YEAR})$	3.616	2.975	3.500	0.020
SITE	1.692	1.000	4.871	0.030
SP	38.376	8.944	3.818	<0.001
Selected model	156.761	37.022	12.194	<0.001

¹This tests whether the non-linear (smoothed) form of the variable better fits the data than its linear form.

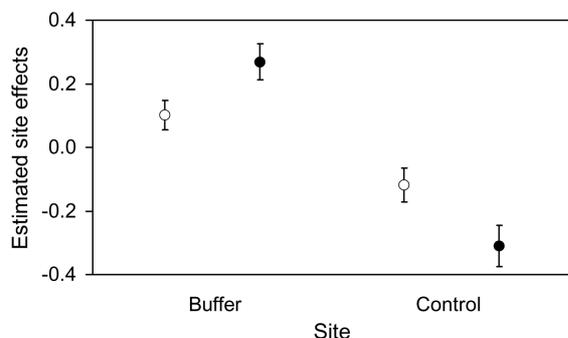


Figure 5. Estimated effects (± 1 SE) of each site on adult capture rates in the riparian buffer strip and the control in 1994–97 for the generalised additive local (open circle) and regional (closed circle) density models. Capture rates are significantly higher in the riparian buffer strip in both models.

0.001). In the local density model, territory density and species had more influence on capture rates, and the site effect was less significant than in the regional density model. However, both models were still highly significant.

The influence of territory density differed among models. Capture rates were positively correlated with territory density in the regional model. In the local model, density had a non-linear effect on capture rates, because of the influence of the very high densities of Least Flycatcher in the riparian buffer strip.

Capture rates varied among species (Table 4). Black-capped Chickadee, Ovenbird and White-throated Sparrow (both models), and Tennessee Warbler, Yellow-bellied Sapsucker and Yellow-rumped Warbler (local model) were captured more frequently than expected, while Red-eyed Vireo was captured less frequently than expected (both models).

Table 6. Analysis of deviance table for the selected regional density model of juvenile capture rates of forest-nesting species in the riparian buffer strip and the control in 1994–97. The selected local density model is $s(\text{LOCAL}) + \text{SITE} + \text{SP}$ and fitted the data as well as the regional model. The symbol $s()$ stands for smoothing spline and signifies that the variable has a non-linear effect.

Variable	Δ deviance	Δ d.f.	F-ratio	P
Smoothing of REGION ¹	0.465	3.017	0.645	0.593
REGION	2.023	1.000	8.711	0.006
Smoothing of YEAR ¹	<0.001	0.008	0.005	0.040
$s(\text{YEAR})$	0.159	2.992	0.217	0.883
SITE	1.661	1.000	7.153	0.012
SP	10.723	15.000	3.078	0.003
Selected model	18.577	17.000	4.705	<0.001

¹This tests whether the non-linear (smoothed) form of the variable better fits the data than its linear form.

Juveniles

We captured 40 juveniles of 12 species in the control, over four years. We captured more juveniles in the riparian buffer strip than in the control in the first three years after harvest (Table 1). However, as for adults, capture rates in the control site were correlated with local and regional territory density (Spearman's rank correlation, $r \geq 0.42$, $n = 25$, $P \leq 0.071$). For this reason, we used GAMs to take into account the effects of territory density on capture rates.

Capture rates were indeed higher in the riparian buffer strip than in the control, whether we accounted for local or regional density using GAMs (Figure 6). Capture rates also were influenced by species and territory density and did not vary significantly among years (Table 5). The effect of regional territory density on capture rates was positive and linear. In contrast, local territory density had a non-linear effect on capture rates. However, as for adults, this was largely attributable to a very high density of Least Flycatchers in the riparian buffer strip.

Species captured more frequently than expected in both local and regional territory density models were Yellow-bellied Sapsucker, Ovenbird and Dark-eyed Junco. The two models fitted the observed capture rates equally well (analysis of deviance, $F_{3,01} = 2.26$, $P = 0.101$).

Discussion

We predicted that 1) the corridor function of the riparian buffer strip would decrease with the gradual regeneration of the adjacent clearcut, and that 2)

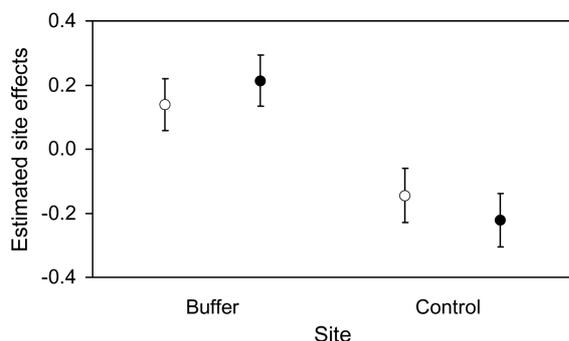


Figure 6. Estimated effects (± 1 SE) of each site on juvenile capture rate in the riparian buffer strip and the control in 1994–97 for the generalised additive local (open circle) and regional (closed circle) density models. Capture rates were significantly higher in the riparian buffer strip in both models.

movement rates would increase in the clearcut as the forest regenerates. We still expected movements to be more frequent in the riparian buffer strip than 3) in the regenerating clearcut, or 4) in a control site. Results differed between juveniles and adults: predictions 1, 2 and 4 were supported for juveniles, whereas prediction 4 and (to some degree) predictions 1 and 2 were supported for adults. Responses also varied among species. For example, the Red-eyed Vireo tended to be captured less frequently than expected based on its territory density, probably because this species spends most of its time singing and foraging in the canopy. However, GAMs allowed us to account for species-specific variation in responses when estimating site and year effects on capture rates.

Adult movements

Variations in capture rates among years in the riparian buffer strip were not significant when including local density as a covariate, but they were when regional density was entered instead. The fact that local density was a significant predictor of capture rates suggests that captures represent movements by birds holding a territory near the net lane and that their use of the riparian buffer strip did not change among years. When we consider regional density instead, the movements decreased after a peak in captures in 1995. However, capture rates remained significantly higher in the riparian buffer strip than in the control site in all post-harvest years, independent of territory density. These results suggest that the riparian buffer strip acted as a movement corridor for adult forest birds. This conclusion differs from that reached by

Machtans et al. (1996) using more conventional statistical methods.

To be called a movement corridor, a linear link must facilitate movements of individuals (Koford et al. 1994). Our design does not permit us to determine whether species exclusively observed or captured in the riparian buffer strip, like the Ovenbird, would use the regenerating clearcut for movements in the absence of a forested link between forest patches. However, the riparian buffer strip apparently funnelled forest bird movements because capture rates were always higher there than in the control site and, in that sense, the buffer strip retained its corridor function even though capture rates eventually returned to pre-harvest levels. Our results are thus consistent with the observation that an open space such as a recent clearcut can cause a barrier effect on adults, as observed by Haas (1995); Desrochers and Hannon (1997); Rail et al. (1997); St. Clair et al. (1998). However, our study may not be comparable those cited above because species and methods differed. Among the three species studied by Haas (1995), the American Robin was present in our study area but was not captured in the regenerating clearcut in the last two years. The three other studies are gap-crossing experiments Black-capped Chickadee mobbing calls (Desrochers and Hannon 1997; St. Clair et al. 1998) or playback of conspecific songs (Rail et al. 1997). The response of birds to these external stimuli, or responses obtained during winter (St. Clair et al. 1998), may produce different results than the stimulus for post-breeding or natal dispersal.

The decreasing sharpness of the edge between the buffer strip and the regenerating clearcut was probably one of the factors contributing to the decrease in adult capture rates between 1995 and 1997 in the buffer strip. Owing to the fast regeneration of woody vegetation we observed in the clearcut, we expected that the permeability of the forest/clearcut edge would increase over time. We expected some species to start using the regenerating clearcut early (e.g., White-throated Sparrow), whereas others used the regenerating clearcut much earlier than expected (e.g., six captures of adult Least Flycatchers in the regenerating clearcut in 1996). The species showing the greatest increase in clearcut use over the duration of the study was the Mourning Warbler. This species started to establish territories in the regenerating clearcut as early as the third year post-harvest, when density reached 9 territories/10 ha, and capture rates were the

highest of all species captured in the regenerating clearcut in 1996 and 1997.

The number of species observed or captured in the regenerating clearcut increased over the four years post-harvest. Clearcut regeneration thus appears to contribute to the restoration of connectivity levels similar to pre-harvest times, at least for species like Mourning and Tennessee Warblers and White-throated Sparrow. The White-throated Sparrow is a habitat generalist (Falls and Kopachena 1994) and the Mourning Warbler nests in dense shrubby areas with or without forest nearby (Pitocchelli 1993). Therefore, we expected these species to start using the new habitat as the forest regenerated and thus, to be captured more frequently. However, half of the species captured in the regenerating clearcut did not have territories in that habitat, indicating that many of the birds captured may have used the regenerating clearcut during off-territory explorations or dispersal movements. Other species (see Connectivity in harvested forest landscapes) were never observed or captured in the regenerating clearcut, however, suggesting that large-scale forestry could severely reduce connectivity for these species.

Juvenile movements

The dispersal movements of juveniles and adults differ in many respects, suggesting that both types of dispersal are subject to different selection pressures (Johnson and Gaines 1990). For example, juveniles disperse farther than adults (Greenwood and Harvey 1982; Paradis et al. 1998) and female birds tend to disperse farther than males (Greenwood 1980; Clarke et al. 1997). Therefore, it is not surprising that landscape configuration affected juvenile and adult dispersal differently.

Post-harvest capture rates in the riparian buffer strip remained higher than pre-harvest levels, indicating that the riparian buffer strip was still acting as a movement corridor for juveniles four years after experimental clearcutting. The fact that there were no significant relationships between capture rates and either local or regional densities indicates that most juveniles captured in the riparian buffer strip were dispersers, in contrast to adults.

The riparian buffer strip acted as a movement corridor for juveniles, but this role gradually decreased with time since clearcutting, except in the fourth year post-harvest, when captures increased both in the riparian buffer strip and in the regenerating clearcut.

We cannot perform post-hoc multiple comparison analyses on GAMs, but the standard error bars in Figure 2 suggest that the increase in the last year was not statistically significant. Nevertheless, the general downward trend in capture rates in the riparian buffer strip, coupled with the increase in capture rates in the regenerating clearcut, support the prediction that some individuals of some species stop to perceive the clearcut as hostile habitat and start using it as a medium for dispersal.

Contrary to our prediction, capture rates in the regenerating clearcut became higher than in the riparian buffer strip in 1997. The timing of captures also differed between the two sites in the fourth year post-harvest, with an increase in captures in early August in the clearcut. This late increase in captures may correspond to a different stage of postfledging dispersal. For example, after leaving their natal area, juvenile Wood Thrushes (*Hylocichla mustelina*) were found in successional stands with dense ground cover (Vega Rivera et al. 1998; Anders et al. 1998). This may explain the higher capture rates we recorded in the regenerating clearcut than in the riparian buffer strip in the fourth year post-harvest. This is also consistent with the fact that not only habitat generalists, but also species generally associated with mature forest, were captured in the regenerating clearcut in 1997 (Black-capped Chickadee, Connecticut Warbler and Purple Finch). Vega Rivera et al. (1998) observed that juvenile Wood Thrushes go back to mature forests in late August after dispersing through unsuitable breeding habitat. This suggests that they may be searching for suitable territory sites for the following year. Although this behaviour is likely to be species-specific, it may explain why some individuals of mature forest species were captured in the regenerating clearcut in our study.

Connectivity in managed forest landscapes

Most studies on movements or isolation effects in fragmented forest landscapes have been conducted in agricultural or suburban landscapes (Wegner and Merriam 1979; Johnson and Adkisson 1985; Askins and Philbrick 1987; Askins et al. 1987; Haas 1995; Matthysen et al. 1995; Villard et al. 1995). These landscapes are characterised by the relative permanence of their fragmentation. Managed forest landscapes are more dynamic, with rapid changes in the matrix following harvesting, and therefore must be studied over the longer-term.

Our results indicate that some species still used the buffer strip for movement four years after clearcutting. The forest species captured or defending territories in the riparian buffer strip that were neither observed nor captured in the regenerating clearcut in any of the four post-harvest years were Downy Woodpecker, Philadelphia and Red-eyed Vireos, Red-breasted Nuthatch, Veery, Ovenbird, Canada Warbler and Pine Siskin. Among those, the vireos, Red-breasted Nuthatch and Ovenbird had high densities in the riparian buffer strip, and the Red-eyed Vireo has already been shown to exhibit a reluctance to cross open gaps (Desrochers and Hannon 1997). Thus, the riparian buffer strip apparently played an important role for these forest specialists and it would be interesting to determine how old (or how high) the regenerating forest must be for these species to move across them. A recent study in a fragmented boreal forest (Bayne and Hobson 2001) showed that adult male Ovenbirds could actually move spontaneously across cropfields, crossing gaps of 100–300 m. However, these authors also found that only one of seven males accompanied by young actually crossed a gap, suggesting that fledglings are reluctant to do so. Whether this reluctance persists after fledglings become independent is unknown.

The dispersal phase of juveniles may play a role in the selection of future breeding sites (reviewed by Machtans et al. (1996)). The barrier effect that Machtans et al. (1996) observed in juveniles was short-lived for certain species. This suggests that natal dispersal of these species would not be negatively affected by forestry over the long term, as long as suitable nesting habitat is maintained in the landscape. However, our data do not allow us to determine whether the restoration of connectivity for these species is sufficient to ensure the persistence of their metapopulations in our study area.

We agree with Beier and Noss (1998) that the study design used in this and Machtans et al. (1996) studies is limited by the fact that we could not compare movement rates in the regenerating clearcut in the presence and absence of a forested corridor. Movements across clearcuts to bridge gaps among forest fragments might be more frequent when birds do not have the possibility to use a forested corridor. However, our design still allowed us to observe an increase in juvenile movements in the regenerating clearcut although a forested corridor was available. Another limitation of our design is the lack of replication, which reduces the generality of our results. In

large-scale experiments such as this one, replication would be very costly. In this study, we chose to focus our efforts on temporal variations in movement patterns in a changing landscape, rather than on the spatial variation in movement patterns in several landscapes with different configurations. The same site will be revisited in the future to determine whether matrix permeability is still relatively low for some forest specialists.

Our study cannot demonstrate that the facilitation of juvenile movements provided by the riparian buffer strip actually increased population viability of the corresponding species over the long term. Ongoing monitoring of the bird communities in the forest fragments connected to the riparian buffer strip will reveal whether this enhanced movement translates into greater population persistence of sensitive species (F. Schmiegelow and S. Hannon, unpubl. data). Our study still shows that even though the use of a riparian buffer strip for movements can be reduced by forest regeneration, it still maintains connectivity for some forest specialists. For these species, corridors may be critical. We agree with Beier and Noss (1998) that the burden of proof of the conservation value of corridors should be shifted to the demonstration of their detrimental effects on the viability of populations of sensitive species in fragmented landscapes.

Our study does not address a related question, i.e., whether maintaining or restoring physical connections among habitat patches is a better conservation approach than allocating the same resources to the enlargement or protection of pristine habitat patches. Two recent approaches seem to hold promise in this respect: experimental translocations (Bélisle et al. (2001), Gobeil and Villard, unpubl.) for larger, wide-ranging taxa, and experimental model systems encompassing metapopulations of small taxa operating over fine scales. Further research in these areas should be encouraged.

Acknowledgements

This research was supported by an Industrial Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) and Alberta-Pacific Forest Industries (AIPac) to IR, by Université de Moncton scholarships to IR, and by a NSERC-Canadian Forest Service-AIPac research

grant to Susan J. Hannon and M-A V. We thank our hard-working assistants, Jean-François Gobeil and Jonathan Hornung. Susan J. Hannon and Fiona K. A. Schmiegelow provided advice and logistical support for the study. We also thank Kari Stuart-Smith, Karl Larsen, and Daryll Hebert from AlPac for their support throughout this project, and André Desrochers, Phil Taylor, and Michael Craig for insightful suggestions on the manuscript.

Appendix. List of bird species mentioned in this article with their scientific names (American Ornithologists' Union 1998) and codes (Pyle 1997).

English name	Code	Scientific name
Yellow-bellied Sapsucker	ybsa	<i>Sphyrapicus varius</i>
Downy Woodpecker	dowo	<i>Picoides pubescens</i>
Hairy Woodpecker	hawo	<i>Picoides villosus</i>
Three-toed Woodpecker	ttwo	<i>Picoides tridactylus</i>
Western Wood-Pewee	wewp	<i>Contopus sordidulus</i>
Alder Flycatcher	alfl	<i>Empidonax alnorum</i>
Least Flycatcher	lefl	<i>Empidonax minimus</i>
Blue-headed Vireo	bhvi	<i>Vireo solitarius</i>
Philadelphia Vireo	phvi	<i>Vireo philadelphicus</i>
Red-eyed Vireo	revi	<i>Vireo olivaceus</i>
Blue Jay	blja	<i>Cyanocitta cristata</i>
Black-capped Chickadee	bcch	<i>Poecile atricapillus</i>
Red-breasted Nuthatch	rbnu	<i>Sitta canadensis</i>
Brown Creeper	brcr	<i>Certhia americana</i>
Winter Wren	wiwr	<i>Troglodytes troglodytes</i>
Veery	veer	<i>Catharus fuscescens</i>
Swainson's Thrush	swth	<i>Catharus ustulatus</i>
Hermit Thrush	heth	<i>Catharus guttatus</i>
American Robin	amro	<i>Turdus migratorius</i>
Cedar Waxwing	cedw	<i>Bombycilla cedrorum</i>
Tennessee Warbler	tewa	<i>Vermivora peregrina</i>
Yellow Warbler	ywar	<i>Dendroica petechia</i>
Magnolia Warbler	mawa	<i>Dendroica magnolia</i>
Yellow-rumped Warbler	yrwa	<i>Dendroica coronata</i>
Ovenbird	oven	<i>Seiurus aurocapillus</i>
Northern Waterthrush	nowa	<i>Seiurus noveboracensis</i>
Connecticut Warbler	conw	<i>Oporornis agilis</i>
Mourning Warbler	mowa	<i>Oporornis philadelphia</i>
Common Yellowthroat	coye	<i>Geothlypis trichas</i>
Wilson's Warbler	wiwa	<i>Wilsonia pusilla</i>
Canada Warbler	cawa	<i>Wilsonia canadensis</i>
Western Tanager	weta	<i>Piranga ludoviciana</i>
Chipping Sparrow	chsp	<i>Spizella passerina</i>
Clay-colored Sparrow	ccsp	<i>Spizella pallida</i>
Le Conte's Sparrow	lensp	<i>Ammodramus leconteii</i>
Nelson's Sharp-tailed Sparrow	nsts	<i>Ammodramus nelsoni</i>
Song Sparrow	sosp	<i>Melospiza melodia</i>
Lincoln's Sparrow	lisp	<i>Melospiza lincolnii</i>
Swamp Sparrow	swsp	<i>Melospiza georgiana</i>
White-throated Sparrow	wtsp	<i>Zonotrichia albicollis</i>
Dark-eyed Junco	deju	<i>Junco hyemalis</i>
Red-winged Blackbird	rwbl	<i>Agelaius phoeniceus</i>
Brown-headed Cowbird	bhco	<i>Molothrus ater</i>
Purple Finch	pufi	<i>Carpodacus purpureus</i>
Pine Siskin	pski	<i>Carduelis pinus</i>

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