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CORRIDORS MAY NOT IMPROVE THE CONSERVATION VALUE OF SMALL RESERVES FOR MOST BOREAL BIRDS

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Abstract. Building or maintaining corridors in fragmented landscapes may be an important method to conserve gap-sensitive species that avoid crossing gaps in forest cover. We tested the effectiveness of corridors by examining the changes in abundance of boreal birds pre- and post-logging in experimental 10-ha and 40-ha reserves that were isolated or connected by corridors, relative to their abundance responses in continuous forest (reference sites). Prior to the analysis, we categorized birds as to their predicted gap sensitivity based on two measures: their use of corridors and gap-crossing behavior in small-scale trials, and their habitat affinities (forest species vs. habitat generalists). The abundance of forest species as a group was consistently higher in reference reserves than in isolated or connected reserves after harvest, except for the first year after harvest, when crowding occurred in isolates. Habitat generalist species showed no differences in abundances across reserve types. As a group, resident species were more abundant in reference and connected reserves than in isolates in three of five years post-harvest, suggesting that corridors might benefit these species. None of the single species analyzed showed consistent evidence of benefiting from corridors. Although four species were most abundant in connected reserves after harvest, their abundances were not significantly lower in isolates than in reference sites. Behavioral classification (gap-crossing propensity) was not useful in classifying single species as to how gap sensitive they would be in response to our experiment: habitat affinity was a better predictor. We suggest that corridors may be useful to retain resident birds on harvested landscapes, but that corridors connecting small reserves of forest are unlikely to offset the impacts of fragmentation for most boreal birds. Assessments of the utility of corridors must, however, be done in the context of the full plant and animal communities that live in the boreal forest.

Key words: boreal birds; boreal mixedwood forest; clearcuts; conservation value; corridors; fragmentation; gap sensitivity; habitat generalists; landscape connectivity; logging; old-forest specialists; reserve size.

Introduction

Improving landscape connectivity could promote the retention of some species in landscapes altered by habitat fragmentation (Merriam 1991, Taylor et al. 1993). However, the importance of corridors in promoting connectivity has been controversial, and some negative effects of connectedness have been identified (Simberloff et al. 1992). In a recent review, Beier and Noss (1998) examined over 30 studies that assessed the utility of corridors for terrestrial vertebrates. Only one-third of the studies provided evidence that corridors enhanced landscape connectivity. Similarly, Desrochers et al. (1999) evaluated the strengths and weaknesses of approaches used to study movement of songbirds in fragmented forests. Both reviews criticized the design and interpretation of many studies and noted a lack of experimental tests of the efficacy of corridors. Overall, carefully controlled experiments that measure the demographic effects of connecting habitat fragments with corridors, coupled with observational studies of individual movements through fragmented landscapes, seem to be the best approach (Haddad 2000).

Species vary considerably in their propensity to cross gaps in the forest canopy (Desrochers and Hannon 1997, St. Clair et al. 1998, Grubb and Doherty 1999), and the gaps themselves differ enormously in vegetation structure and composition across landscape types. Given the rapid rate of habitat loss and degradation in forested ecosystems, we have little time to conduct research on all forest species and must search for ways to group or rank responses to forest fragmentation (Hansen and Urban 1992, Hansen et al. 1993, Villard and Taylor 1994, Desrochers et al. 1999). A number of recent studies have attempted to quantify experimentally the relative propensities of different species to cross gaps of different types and widths (Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998, Bélisle 2000). These studies may aid conservation planning if they can be extrapolated to predict demographic change for species inhabiting fragmented forests (Desrochers et al. 1999).

Since 1993, we have been conducting studies in the

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boreal mixedwood forest of north-central Alberta, Canada to evaluate the effects of forest fragmentation by clear-cutting on forest songbirds (reviewed in Schmiegelow and Hannon 1999). One component of the ''Calling Lake Fragmentation Project'' is a large-scale replicated experiment in which forest reserves of different sizes were isolated by clear-cutting. Community composition and species abundances have been monitored pre- and post-harvest in forest reserves and unharvested reference sites (Schmiegelow et al. 1997). Reserves are of two types: isolated (surrounded by clear-cutting on all sides) and connected (surrounded by clear-cutting on three sides, with the fourth side connected to a 100 m wide riparian forest buffer strip; such strips are left by forest companies to protect water quality in lakes). In a companion study, birds were mist-netted in the buffer strips and in control areas along lakes to measure whether they used the buffer strips as travel corridors to avoid crossing clearcuts. Adult and juvenile birds of some species used the buffer strips as corridors, but this use declined as the clearcuts regenerated (Machtans et al. 1996, Robichaud et al., *in press*). An a priori prediction of the Calling Lake Fragmentation project was that if the buffer strips were important conduits for dispersal and movement through the landscape, then the reserves connected by corridors should either retain more forest species or should maintain them in greater abundance than in reserves without connections (Schmiegelow and Hannon 1993).

The purpose of this paper is to report changes, up to five years post-harvest, in the breeding season abundance of forest songbirds in connected, isolated, and reference reserves, relative to pre-harvest levels. We assumed that clearcuts would reduce the probability of movement of some species to the isolated reserves, resulting in lowered abundance in the isolates relative to the pre-harvest condition and compared with reference reserves. We predicted that connecting isolates with corridors would increase the probability of birds colonizing or recolonizing them, relative to the fully isolated reserves. We assumed that if the clearcuts were barriers, then fewer birds would return to isolated reserves to breed and fewer juveniles, prospecting for territories in the previous summer or the current spring, would cross the clearcuts to colonize the isolates. Our previous work indicated that resident species might be more sensitive to fragmentation than migrants (Schmiegelow et al. 1997), but there have been numerous studies suggesting that some Neotropical migrant species may also be gap sensitive (reviewed in Desrochers et al. 1999).

Here, we make explicit a priori predictions as to which species were more likely to be affected by isolation (i.e., were gap sensitive) and which were likely to be gap neutral (not affected by isolation). We use two types of data to predict gap sensitivity: (1) behavioral evidence of corridor use and the propensity of birds to fly across gaps in the forest canopy (Machtans et al. 1996, Desrochers and Hannon 1997, Robichaud et al., *in press*); and (2) habitat affinities of species (old-forest specialists, forest species, habitat generalists). We test these predictions using the abundance response of species to our fragmentation experiment.

METHODS

A priori predictions as to gap sensitivity

Gap-crossing behavior.—Gap-crossing behavior was studied at Calling Lake by examining capture rates of birds in mist nets stretched across the buffer strips that connected the reserves, relative to observations of birds crossing the clearcuts that separated reserves (Machtans et al. 1996), or relative to capture rates in mist nets placed in the clearcuts between reserves (Robichaud et al., *in press*). A second study, conducted in Quebec, Canada, measured the propensity of species to cross forest gaps of varying widths using playback experiments (Desrochers and Hannon 1997). We defined gap sensitive species as those that were never or very rarely seen crossing clearcuts, but were captured in mist nets in the buffer strip (Table 1). We also included species that had $<50\%$ probability of crossing a gap of 60 m (Desrochers and Hannon 1997: Fig. 2). Gap-neutral species were those frequently observed crossing clearcuts by Machtans et al. (1996) or captured in clearcuts by Robichaud et al. (*in press*).

Habitat affinities.—All of the species examined in this paper are commonly found breeding in older forests in our area. After logging, some of these species colonized the regenerating cutblocks between the reserves. We defined a clearcut colonist as a species that was observed $\geq 20\%$ as frequently in clearcuts as in older forest reference areas in point counts conducted in 1997 and 1998 (F. K. A. Schmiegelow and S. J. Hannon, *unpublished data*). Species that did not colonize clearcuts were termed forest species and those that colonized clearcuts were termed habitat generalists. We further classified the forest species as to their affinities for old-growth forest using data from Schieck et al. (1995), who compared densities of birds in pyrogenic aspen forest in northern Alberta categorized as young (20–30 yr), mature (50–65 yr), and old (≥ 120 yr). We defined old-forest specialists as those forest species found at highest abundances in old forest and rarely or never found in younger seral stages. The remaining forest species were found in all seral stages (Schieck et al. 1995). We predicted that old-forest specialists and forest species would be gap sensitive, because the clearcuts represent nonhabitat to them, and that habitat generalists would be gap neutral, because the regenerating clearcuts are used as habitat (Table 1).

Study area and experimental design

We conducted the study in a ~140-km^2 block of boreal mixedwood forest west of Calling Lake (55° N, 113° W), in north-central Alberta, Canada. The upland

TABLE 1. A priori classification of gap sensitivity of boreal birds based on gap-crossing propensity and habitat affinity.

Gap sensitivity, by species	Gap-crossing propensity	Habitat affinity†
Gap sensitive (GS)		
Ovenbird, *Seiurus aurocapillus*	GS	f (GS)
Black-throated Green Warbler, *Dendroica virens*		o (GS)
Western Tanager, *Piranga ludoviciana*		o (GS)
Yellow-rumped Warbler, *Dendroica coronata*	GS	f (GS)
American Redstart, *Setophaga ruticilla*		f (GS)
Gap neutral (GN)		
Red-eyed Vireo, *Vireo olivaceus*	GS	g (GN)
White-throated Sparrow, *Zonotrichia albicollis*	GN	g (GN)
Mourning Warbler, *Oporornis philadelphia*	GN	g (GN)
Yellow-bellied Sapsucker, *Sphyrapicus varius*	GN	g (GN)
Chipping Sparrow, *Spizella passerina*		g (GN)
Connecticut Warbler, *Oporornis agilis*		g (GN)

† Key to abbreviations for habitat affinity: o, old-forest specialist; f, forest species; g, habitat generalist.

mixedwood in this area consists of aspen (*Populus tremuloides*) mixed with white spruce (*Picea glauca*), in a larger landscape mosaic of lakes, wetlands, and treed bogs (black spruce, *P. mariana*, and larch, *Larix laricina*). Approximately 21% of the area is composed of natural nonforested land (lakes, wetlands). Broad-scale harvesting of aspen, primarily for pulp and paper production, dates back to 1992 in Alberta. Over 75% of the mixedwood has been allocated for timber production. The forest is clear-cut in alternating blocks of 10–60 ha, with a rotation period of 40–70 yr. Timber is taken out in 2–3 passes, with the second pass occurring ~10 yr after the first pass. Forested buffer strips 100 m wide are left around permanent lakes. The study area, our experimental design, and natural and anthropogenic disturbances are described in more detail in Schmiegelow et al. (1997) and Schmiegelow and Hannon (1999).

Study sites were located in old (80–130 yr) aspen stands with <20% overstory spruce and are part of the ‘‘Calling Lake Fragmentation Project’’ of Schmiegelow et al. (1997) (Fig. 1). Here, we report on bird abundances in isolated, connected, and reference forest reserves of 10 ha and 40 ha in size, each replicated three times. Connected and isolated reserves were created in the winter of 1993–1994 by clear-cutting a minimum 200-m strip on all four sides of isolates and on three sides of connected reserves. The fourth side of the connected reserves was continuous with a 100 m wide forested buffer strip left along lakes (Fig. 1). Up to 2–3% of live trees were left in clumps in clearcuts surrounding the reserves. Reference reserves were embedded in ~4000 ha of unlogged forest that runs through the center of the study area (Fig. 1). Overall, 13% of the forest present in the study area prior to the experiment was harvested in 1993–1994, and an additional 2% had been harvested in 1982.

Beier and Noss (1998) noted that corridor presence is often correlated with other variables (e.g., patch size, landscape context), thus confounding analyses of the effects of connectedness. We used an experimental approach with a Before-After-Control-Impact design (Green 1979, Stewart-Oaten et al. 1986) that held patch size constant over time (i.e., pre- and post-harvest) and altered connectedness. Hence, corridor presence is not confounded with patch size. Although we only had one year of pre-harvest data and annual variability in bird abundance is high, we monitored reference reserves throughout the study in order to control for temporal variation. Our pre-harvest year controls primarily for possible differences in initial conditions across reserves.

We used corridors of riparian forest because rules for forestry operation in this region dictate that these must be left for protection of water quality. Thus, our connected reserves were closer to riparian areas than were isolates or reference reserves. However, we believe that the influence of the riparian zone was minimal, as edge influence on vegetation structure and composition from lakeside riparian zones usually only penetrates up to 40 m (Harper 1999), and other edge effects (increased nest predation and altered bird abundances) are minimal in this system, at least at clearcut edges (Song 1998, Cotterill and Hannon 1999, Song and Hannon 1999). We controlled for differences in tree composition (age and percentage of conifers) across our study area by stratifying across replicate groups and size classes within the treatments and reference sites.

Bird sampling

Songbirds and woodpeckers were sampled at permanent sampling stations set out 180–200 m apart: 10-ha reserves had two stations and 40-ha reserves had eight stations. Stations were ≥100 m from the reserve edge. Birds were sampled at each station using 5-min point counts (Ralph et al. 1993) with a 100 m radius, visited five times, at 10-d intervals, from the third week

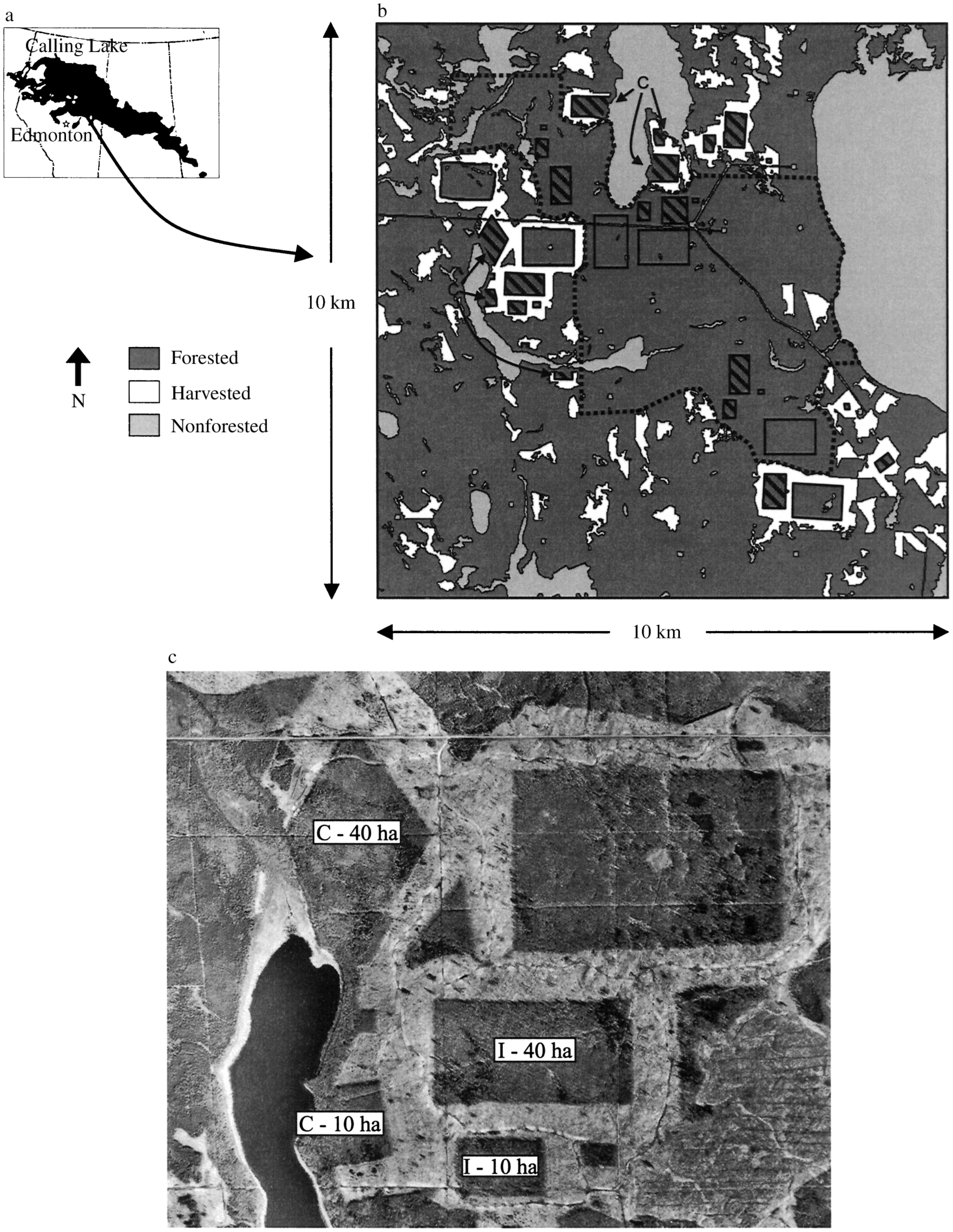

FIG. 1. (a) Location of the Calling Lake study area in central Alberta, Canada; the boreal mixedwood is shaded. (b) Layout of the Calling Lake Fragmentation Study with 10-ha and 40-ha reserves hatched; 1-ha and 100-ha reserves were not used in this study. The reference area is outlined with a dashed line. (c) Aerial view of part of the study area showing 10-ha and 40-ha riparian connected (C) and isolated (I) reserves.

of May through early July each year. Each survey round took 2–5 d. Point counts were conducted between sunrise and 1000 h in fair weather (no rain, and wind speeds <25 km/h, i.e., Beaufort level 5: small branches move). Observers were rotated among reserves and the order of sampling stations was varied over each round to avoid biases. Sampling started in the year prior to harvesting (1993) and continued for five seasons post-harvest (1994–1998).

Data reduction and compilation

The relative abundance of each bird species in each reserve was compiled by taking the maximum number of individuals recorded in any single visit, over the five sampling rounds in each year. Data were first weighted using evidence of probable breeding activity (Schmiegelow et al. 1997: Table 1). For example, a singing or countersinging male was weighted as 1.0, a calling male or female as 0.5, a pair as 2.0, and birds observed to be nesting as 2.0. Observations were weighted to avoid inflating the number of breeding birds recorded (e.g., some singing males may be unmated) and are thus a conservative estimate of abundance. We also consider our abundance estimates to be relative, because the point-count technique does not provide absolute measures of abundance.

Rare or transient species (<30 individuals present over all reserves pooled pre-harvest) and riparian species (e.g., Red-winged Blackbirds, *Agelaius phoeniceus*) were deleted from the data set. Data were pooled into two groups, forest species and habitat generalists (see Appendix), for one set of analyses. Because resident species were relatively rare, we also pooled these for analyses, as they were subjected to similar winter conditions on the study area. For single-species analyses, we deleted species with fewer than 10 individuals in reference reserves prior to harvesting, because we planned to compare abundance changes on treatment reserves from pre- to post-harvest relative to changes on reference reserves.

Data analysis

To avoid pseudoreplication, our unit of analysis is the reserve, not the sampling station. Data were analyzed in two ways. First, we used a repeated-measures ANOVA with year as the within-subjects factor and treatment (reference, isolated, or connected reserve) as the between-subjects factor. Annual abundances post-harvest were compared with the pre-harvest abundances, in order to test for year × treatment interactions. Initially, reserve size was entered as a covariate, but because reserve size × treatment interactions were not significant, reserve size was not included in final models. To avoid Type II errors due to small sample sizes and to be cautious in our interpretation of potential impacts of fragmentation, we considered $P < 0.10$ to be statistically significant.

To be biologically significant, treatment effects should exceed natural or background variation found on reference sites (e.g., Wiens 1995). Hence, we developed a second analysis method, based on the natural background variation in our reference reserves, to determine how large treatment effects should be to be considered biologically significant. First, we pooled annual abundances for each species across all reference sites. We then calculated mean abundance for each species over the six years analyzed here. The background variation in abundance over the six years was calculated by dividing the largest single deviation in annual abundance by the mean abundance, for each species (analogous to a coefficient of variation). For example, the mean abundance of Ovenbirds (*Seirus aurocapillus*) in reference reserves over six years was 44.5 birds and ranged from 33 to 61 birds. The largest deviation in any year was 16.5 ($61 - 44.5$) birds, resulting in a 37% departure from the mean for Ovenbirds ($16.5/44.5 \times 100 = 37\%$). The percentage deviations (background variation) for each species are reported in Table 2. To quantify treatment effects, we first calculated the annual abundances of each species in each reserve type (isolated or connected). We then calculated the annual proportional change from pre-harvest abundance ($t = 1993$) by dividing abundance in year$_{t+x}$ by abundance in year$_t$, for each treatment. Proportional changes less than 1.0 indicated a decline from pre-harvest conditions; those >1.0 indicated an increase from pre-harvest conditions. Differences in proportional changes between treatments that exceeded the background variation in the references were considered biologically relevant. We call this the effect size (ES) method. We report results of both analysis techniques (Table 2); however, we evaluate our results using the ES method, because power was low for several species and we wished to assess biological significance. To be conservative in our interpretations, we also noted when differences occurred within 5% of the ES.

RESULTS

A priori gap sensitivity classifications

We assigned each of the 11 species for which we had sufficient data to analyze as gap sensitive or gap neutral according to their gap-crossing propensities and habitat affinities (Table 1). There was a fairly good concordance between the predictions made using gap-crossing behavior and habitat affinity, except for the Red-eyed Vireo (*Vireo olivaceus*).

Abundance responses in isolated reserves

We first compared the relative abundances of pooled and single species on the reference sites with those in the isolated reserves, to assess responses to isolation. As a group, forest species did not exceed pre-harvest levels, but their abundance was consistently higher in reference reserves, with the exception of crowding in the isolates in the first year post-harvest (Table 2, Fig.

TABLE 2. Percentage variation and range of abundance in reference reserves and reserve type (C, connected; I, isolated; R, reference) with the highest abundance, using the Effect Size (ES) method.

Species used in analysis	Variation (%) in reference reserves (ES)	Abundance range in references (n = 6 yr)	Reserve type with highest relative abundance (no. years)†	P for yr × trt interaction from ANOVA	Treatment effect with ES method?‡
Forest species grouped	13	186–240	R (4)	<0.001	yes
Habitat generalists grouped	31	109–180	=	0.32	no
Residents grouped	45	17–42	R (4)	0.91	yes
Ovenbird	37	33–61	=	0.32	no
Black-throated Green Warbler	37	11–22	R (2)	0.16	yes
Western Tanager	56	4–14	RC (2)	0.15	yes
Yellow-rumped Warbler	46	35–69	R (1)	0.05	yes (NC)
American Redstart	127	2–10	NP	0.51	no
Connecticut Warbler	40	12–27	C (2)	0.53	yes
Red-eyed Vireo	69	16–24	C (4)	0.10	yes
White-throated Sparrow	25	27–44	C (2)	0.63	yes
Mourning Warbler	26	15–22	C (3)	0.58	yes
Yellow-bellied Sapsucker	29	6–11	RI (3)	0.32	yes
Chipping Sparrow	53	10–21	NP	0.28	yes (NC)

Notes: For detailed information on annual abundance changes, see Figs. 2–5. See Appendix for scientific names.

† Reserve type with highest relative abundance using ES method; "=" indicates that no difference between reserve types was detected; NP, no pattern was detected in which reserve type had higher relative abundance.

‡ NC, no consistent effect of treatment over years.

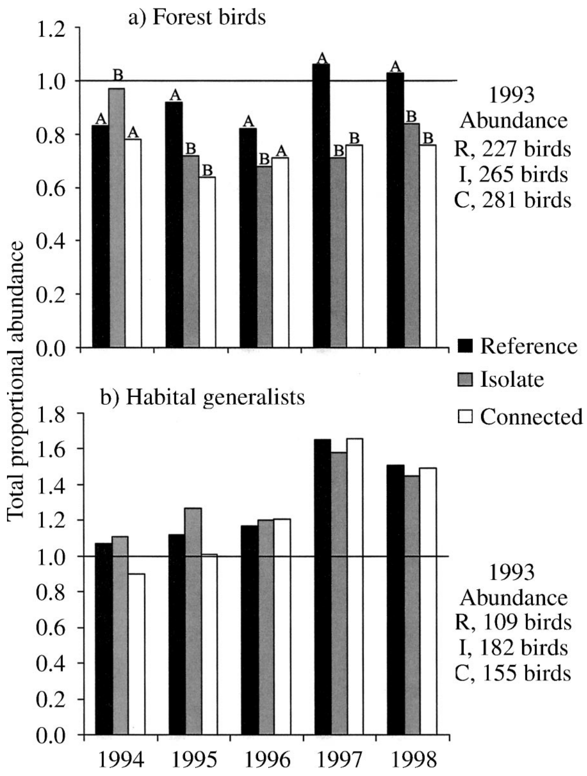

FIG. 2. Post-harvest abundances of (a) forest birds and (b) habitat generalists relative to pre-harvest abundances on the same sites for references (R), isolates (I), and connected (C) reserves. Bars with different letters are significantly different within a year using the Effect Size (ES) method. Groups of bars with no letters on top are not significantly different. Initial abundances in each reserve type pooled prior to harvesting (1993) are indicated to the right of the panels.

2a). Habitat generalists remained at pre-harvest levels in all reserve types from 1994 to 1996, with no difference between reserve types, and then increased above pre-harvest levels in 1997 and 1998 in all reserve types (Table 2, Fig. 2b; year effect (ANOVA), F = 28.9, df = 5, P < 0.001). Resident species had higher abundances in reference reserves than in isolates in four of five years post-harvest (Fig. 3). Resident numbers were highly variable over the 5-yr study period (year effect (ANOVA), F = 10.5, df = 5, P < 0.02). Among individual species, only the Black-throated Green Warbler (*Dendroica virens*) and Western Tanager (*Piranga ludoviciana*) were more abundant on reference reserves than in isolates in more than one year, and this only

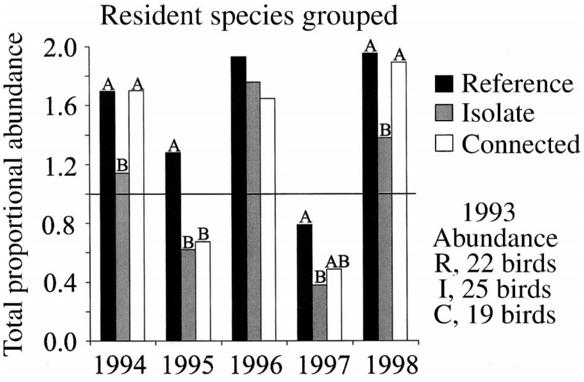

FIG. 3. Post-harvest abundances of resident bird species combined, relative to pre-harvest abundances on the same sites for references (R), isolates (I), and connected (C) reserves. Bars with different letters on top are significantly different within a year using the ES method. Groups of bars with no letters on top are not significantly different. Initial abundances in each reserve type pooled prior to harvesting (1993) are given to the right of the panel.

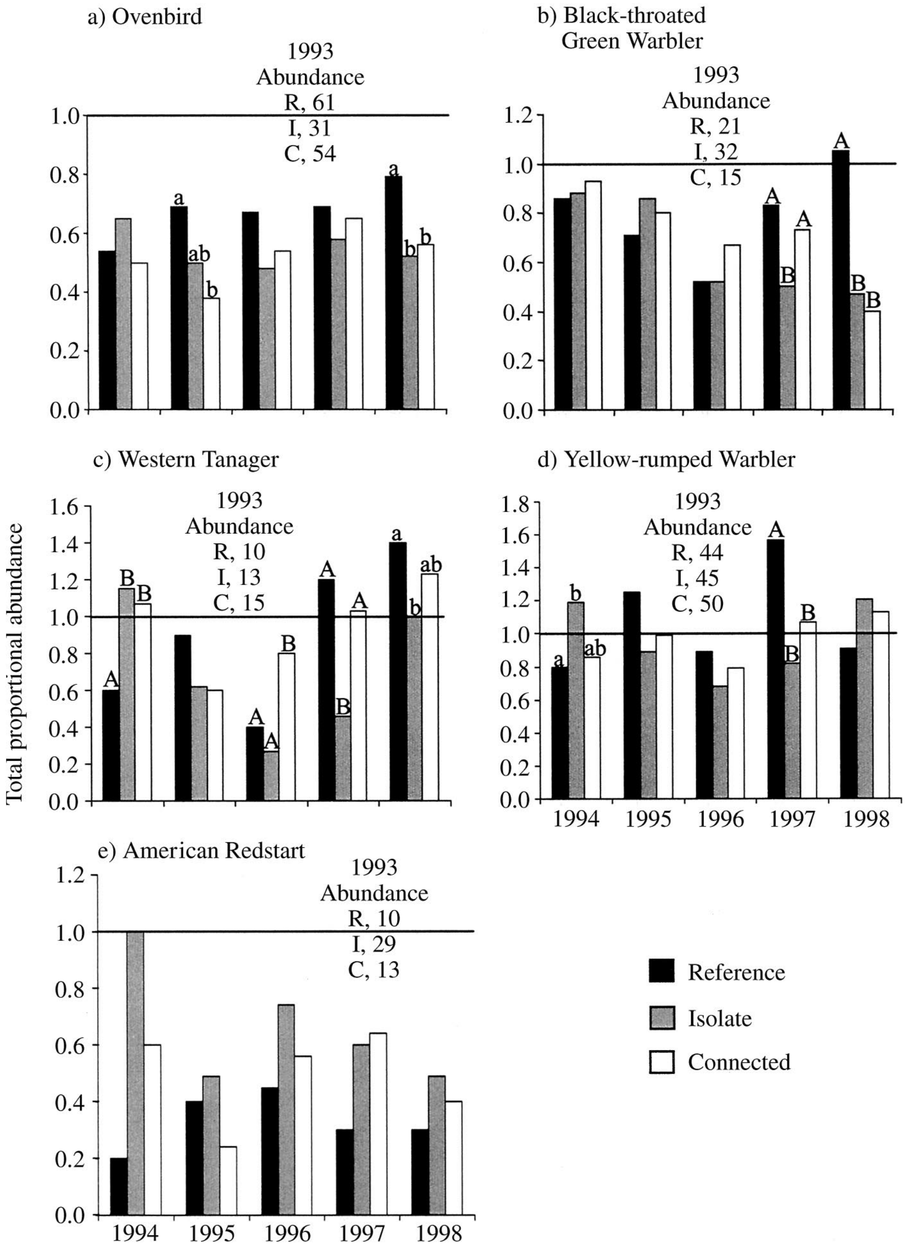

FIG. 4. Post-harvest abundances of bird species predicted to be gap sensitive relative to pre-harvest abundances on the same sites for references (R), isolates (I), and connected (C) reserves. Bars with different letters on top are significantly different within a year using the ES method. Lowercase letters indicate differences within 5% of the ES cutoff. Groups of bars with no letters on top are not significantly different. Initial abundances in each reserve type pooled prior to harvesting (1993) are given above each panel.

occurred in 1997 and 1998 (Table 2, Fig. 4). Yellow-bellied Sapsuckers (*Sphyrapicus varius*) had similar abundances in reference and isolated reserves in three of five years post-harvest, suggesting that they are not gap sensitive (Table 2, Fig. 5). The remaining species showed no consistent pattern of abundance changes on reference sites vs. isolates over the years (Figs. 4 and 5).

Efficacy of corridors

For forest birds as a group, presence of corridors did not increase abundances in connected reserves above those in isolated reserves (Fig. 2). Abundances of resident species in connected reserves were similar to those in reference sites in three of five years, suggesting that corridors may be helpful for these species (Fig. 3). Connecticut Warbler (*Oporornis agilis*), Red-eyed

Vireo, White-throated Sparrow (*Zonotrichia albicollis*), and Mourning Warbler (*Oporornis philadelphia*) showed highest relative abundances in connected reserves; Red-eyed Vireos for four of five years, Mourning Warblers for three of five years, and the other two species in the last two years only (Table 2, Fig. 5). However, because these species were not significantly lower in isolates than in reference sites, we conclude that this may be a habitat effect rather than an effect of the corridor per se. For the remaining species, there was no consistent pattern of abundances across reserve types over years, except for the Western Tanager, which did relatively better in connected reserves than in isolates for three of five years (Fig. 4).

Accuracy of our a priori predictions

Behavioral classification (gap-crossing propensity) was not useful in classifying single species as to how gap sensitive they would be. Habitat affinity was useful in a coarse way: forest birds as a group appeared to be gap sensitive, and resident species, most of which are found in older forest, also appeared to be gap sensitive. Lack of significance at the level of individual species was influenced by relatively small sample sizes and high variation in abundances.

DISCUSSION

Efficacy of corridors

In our original design of the Calling Lake Fragmentation Study, we connected reserves with buffer strips to provide travel corridors for birds moving through the landscape (Schmiegelow and Hannon 1993). We reasoned that providing a connection to more continuous forest on one side of an otherwise isolated reserve would facilitate colonization or recolonization of that reserve after the surrounding area was harvested. We found that during dispersal some species of birds used the corridor for movement and were not observed to fly across the clearcuts (Machtans et al. 1996, Robichaud et al., *in press*). However, although both forest species and resident species, as groups, had lower abundances in the isolated reserves than in the reference sites after isolation by forest harvesting, only resident species appeared to be ''rescued'' by the presence of a corridor to the connected reserves. Of the individual species analyzed, only the Western Tanager and Black-throated Green Warbler appeared to benefit from the presence of a corridor, but this was not consistent over all years. Hence, our results suggest that corridors had limited utility for most species, at least over the short term of our experiment and in a landscape that was still ~67% forested. One caveat of this conclusion is that interannual abundances of most species were quite variable; hence, our ability to detect what we defined to be a biologically significant effect against this natural background variation was limited. As well, we had insufficient data to analyze most species within the community at the individual level.

In an earlier paper (Schmiegelow et al. 1997), we reported results from the same experiment before and two years after harvest. The overall conclusions that we made then are consistent with those of the present study. Although fragmentation effects were detected at that time for some species, the effects were of small magnitude and were most prevalent in the smallest reserves (1 ha and 10 ha). Resident species were highlighted as the group most affected by fragmentation, consistent with research in boreal forests of Fennoscandia (e.g., Helle and Järvinen 1986, Virkkala et al. 1994). In addition, gap-crossing experiments conducted in winter on resident birds indicate that they use corridors in preference to flying across open fields (St. Clair et al. 1998). Hence, despite their rarity compared to migrants (residents comprise only 6% of total bird abundance; Schmiegelow et al. 1997), they are of major conservation concern (see also Schmiegelow and Mönkönnen 2002). Unfortunately, this rarity makes it more difficult to detect changes in abundance of species over time (Carlson 2001).

Most studies on corridor use and isolation effects in birds have been conducted in agricultural landscapes where the matrix structure and composition contrasts highly with the forest patches, and the land use change in the matrix is permanent (e.g., Lens and Dhondt 1994, Haas 1995, Grubb and Doherty 1999). Sieving et al. (1996) found that the structure of the matrix beside forest patches influences the probability of forest birds entering them in response to song playbacks, with denser vegetation being more permeable. In landscapes dominated by forestry, the clearcut matrix regenerates and gaps in the forest are not permanent. The clearcuts in our area have been regenerating quickly (by 1997, the mean height of regenerating trees and shrubs was 173 cm; Robichaud et al., *in press*) and the number of species found singing in the clearcuts has increased from 1994 to the present (Schmiegelow and Hannon 1999). Concomitantly, Robichaud et al., (*in press*) noted a decrease in capture rates of birds in the corridors and an increase in captures in the regenerating clearcuts in late summer four years after harvesting, indicating that more birds were using the clearcuts for dispersal. Other studies have also suggested that dispersing juveniles of some species may use early-successional forest with dense ground cover, such as that found in regenerating cutblocks, for movement (e.g., Anders et al. 1998, Vega Rivera et al. 1998).

Potential confounding factors

We assumed that our treatment effects were primarily related to variation in the connectedness of reserves. However, some forest species may have been deterred from settling in the isolates or connected reserves because of edge effects (e.g., Saunders et al. 1991). Proportionally less edge was created around connected reserves than around isolated reserves. Our point-count stations sampled up to the edges of the reserves; hence,

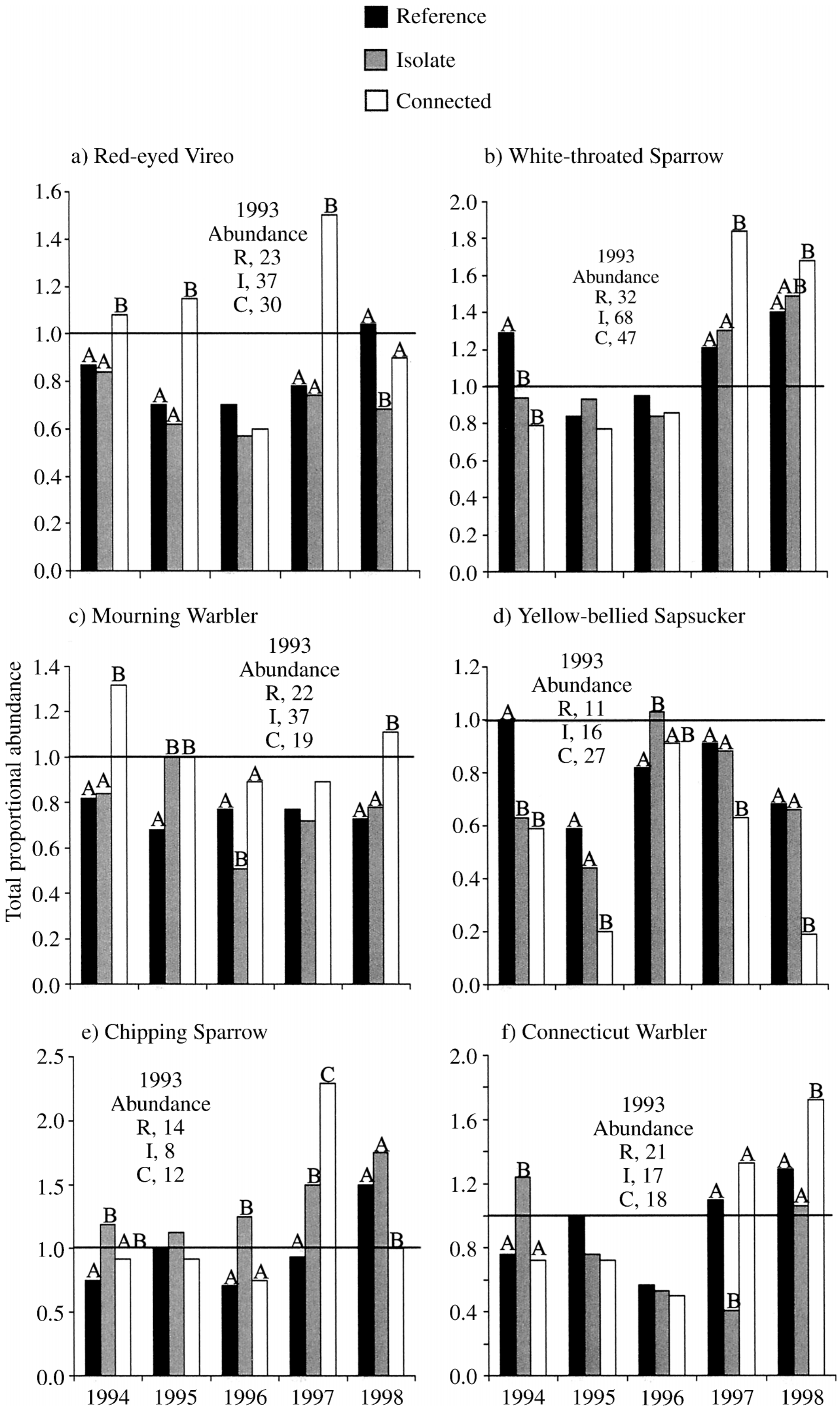

FIG. 5. Post-harvest abundances of bird species predicted to be gap neutral relative to pre-harvest abundances on the same sites for references (R), isolates (I), and connected (C) reserves. Bars with different letters on top are significantly different within a year using the ES method. Groups of bars with no letters on top are not significantly different. Initial abundances in each reserve type pooled prior to harvesting (1993) are above each panel.

some of the habitats sampled could have been altered from the pre-harvest condition and been more attractive to generalist species. Song (1998), working 5 km north of our sites, detected no difference between densities of songbirds at 2-yr-old forest–clearcut edges vs. plots in continuous forest. Hence, we do not believe that our results are confounded by possible habitat changes at edges.

Secondly, some species may have been deterred from settling in isolates or connected reserves due to an increase in nest predation at the forest–clearcut edge or in the whole reserve, as documented for other fragmented forest systems (e.g., Paton 1994). We reject this possibility because we found no increase in predation of artificial nests in fragments compared to references in continuous forest up to five years post-harvest, nor was there a higher nest predation rate at the forest edge when compared to the interior (Cotterill and Hannon 1999, Song and Hannon 1999). In addition, in a study on the reproductive success of American Redstarts (*Setophaga ruticilla*) conducted in the same landscape, we found no increase in predation rate on nests close to clearcut edges (S. J. Hannon and M.-A. Villard, *unpublished data*).

Finally, increased abundances in reference reserves relative to the more isolated reserves could have been due to area sensitivity of some species. Although we cannot discount this possibility, we do not think this is the case for several reasons. The effective size of connected reserves was larger than that of isolates because of the riparian buffer strip adjacent to one side, but for forest species, this did not translate into higher abundances in connected vs. isolated reserves. As well, work in this region has failed to detect avoidance of clearcut edges in boreal passerines (Song 1998, Lambert and Hannon 2000). Moreover, even the small reserves that we studied were sufficient in size to encompass the territories of species included in our analyses. Thus we can rule out most factors that might contribute to area sensitivity, and thereby confound the interpretation of our results.

Predictors of gap sensitivity

We examined two ways of predicting gap sensitivity: behavioral observations of gap-crossing propensities and habitat affinities. Ovenbirds, Yellow-rumped Warblers (*Dendroica coronata*), and Red-eyed Vireos were classified a priori as gap sensitive based on behavioral observations of gap crossing and use of corridors; Ovenbirds, Black-throated Green Warblers, Western Tanagers, Yellow-rumped Warblers, and American Redstarts were classified as gap sensitive due to habitat affinities. Red-eyed Vireos were clearly not gap sensitive, as their highest densities occurred on connected reserves. Of the remaining species classified as gap sensitive, only the Western Tanager, after crowding into isolated and connected reserves in the first year post-harvest, had a pattern of higher relative abundances in reference and/or connected reserves. Hence, either our designations of gap sensitivity based on behavioral data are not appropriate, or the abundances of species that we studied are too variable to detect a difference. For example, Ovenbirds, apart from crowding in the isolates in the first year after harvest, were consistently higher in abundance in reference reserves, but this was neither statistically nor biologically significant, given the background variation in this species. The low predictive power and the logistical constraints to conduct gap-crossing experiments may preclude the widespread use of this technique to assess sensitivity of birds to fragmentation.

All species defined as habitat generalists (Table 2) appeared to be gap neutral. Other studies have also found seral stage or habitat affinity to be good predictors of patch colonization in fragmented landscapes (e.g., Villard and Taylor 1994, Canterbury et al. 2000). Because information on habitat affinity can be derived from broad-scale census techniques, this method of classifying potential sensitivity to one aspect of fragmentation (i.e., habitat isolation) may be useful for entire communities of species.

Conclusions and conservation implications

Gaps created in forest cover by recent clear-cutting appeared to reduce the probability of reaching isolated forest patches for some forest birds, especially residents, at least up to five years post-harvest. Although connecting isolated forest patches with 100 m wide forested corridors did not appear to increase connectivity of the landscape for most species, reduced connectivity will probably be ameliorated over the longer term for species that use young forest as habitat, due to the rapid regeneration of the clearcuts. However, in the managed boreal forest landscape that we studied, there is concern over old-forest specialists, such as the Black-throated Green Warbler, Western Tanager, and several resident species. Under existing harvesting operations, the second pass of logging occurs ~10 yr after the first pass, leaving a landscape of 10-yr-old regeneration and clearcuts, with a few remnant patches of older forest in buffer strips, inoperable areas, and limited small reserve areas. Thus, the impacts of loss of connectivity for old-forest specialists may be more severe after the second pass of logging, although overall habitat loss will probably be a more important factor in causing declines (e.g., Andrén 1994, Fahrig 1997).

The costs and benefits of providing corridors must be evaluated in the context of entire ecosystems. In our study region, 30–100 m wide buffer strips are currently left by logging companies along stream and lake courses for the protection of water quality. Recent research in the boreal mixedwood in this region has questioned the usefulness of providing buffers on all lakes for this purpose (Devito et al. 2000, Prepas et al. 2001). In addition, 100 m or narrower buffer strips do not provide breeding habitat for many forest bird species in this community (Hannon et al., *in press*). Hence, in the longer term, it may be better for conservation of boreal birds to reallocate some of the habitat in buffer strips to increase the size of protected areas of old forest in the landscape, given that some gap-sensitive species are old-forest specialists. These protected areas could be connected to corridors of older forest left along major river courses, which may be used as migration routes. However, management decisions on reallocation of exclusion zones for forestry activities must also take into account the needs of species that may require intact riparian areas for some stage of their life cycle, as well as species that may be more sensitive to reduced landscape connectivity on a fine scale, due to limited dispersal capabilities. Clearly, more research is required on the ecological role of riparian systems in the boreal mixedwood forest before final management decisions as to the efficacy of buffer strips are made. Furthermore, simply considering trade-offs in allocation of very limited protected areas is unlikely to achieve conservation goals. Larger issues of habitat retention have yet to be addressed in this system.

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APPENDIX

A list of boreal bird species used in the analysis, organized by habitat affinity, is available in ESA's Electronic Data Archive: *Ecological Archives* A012-014-A1.