

ARE BOREAL BIRDS RESILIENT TO FOREST FRAGMENTATION? AN EXPERIMENTAL STUDY OF SHORT-TERM COMMUNITY RESPONSES

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Abstract. We studied the effect of habitat fragmentation on the richness, diversity, turnover, and abundance of breeding bird communities in old, boreal mixed-wood forest by creating isolated and connected forest fragments of 1, 10, 40, and 100 ha. Connected fragments were linked by 100 m wide riparian buffer strips. Each size class within treatments and controls was replicated three times. We sampled the passerine community using point counts before, and in each of two years after, forest harvesting, accumulating 21 340 records representing 59 species. We detected no significant change in species richness as a result of the harvesting, except in the 1-ha connected fragments, where the number of species increased two years after isolation. This increase was accounted for by transient species, suggesting that the adjacent buffer strips were being used as movement corridors. Diversity (log series alpha index) was dependent on area in the isolated fragments only after cutting, having decreased in the smaller areas. Turnover rates in the isolated fragments were significantly higher than in similar connected or control areas, due to species replacement. Crowding occurred in the isolated fragments immediately after cutting, but two years after fragmentation, the responses in abundance of species varied with migratory strategy. Numbers of Neotropical migrants declined in both connected and isolated fragments, and resident species declined in isolated fragments. Most species in these groups require older forest, many favoring interior areas. Abundance of short-distance migrants, most of which are habitat generalists, did not change. Overall, although there was no decrease in species richness from our recently fragmented areas, community structure was altered; maintaining connections between fragments helped to mitigate these effects. Nevertheless, the magnitude of the fragmentation effects we documented is small compared with those observed elsewhere. Birds breeding in the boreal forest, where frequent small- and large-scale natural disturbances have occurred historically, may be more resilient to human-induced habitat changes, such as those caused by forest harvesting. However, these results should be interpreted with caution. First, they are short-term and address only broad-scale community responses based on species richness and relative abundance. Second, the study area was embedded in a landscape where large areas of old, mixed forest are still available, potentially dampening any local-scale impacts of fragmentation.

Key words: boreal mixed-wood forest; connectivity; experimental fragmentation; Neotropical migrants; regional forests; songbird communities.

INTRODUCTION

Habitat loss and concomitant fragmentation are concerns central to the conservation of biodiversity. Despite efforts to slow rates of habitat destruction, most ecosystems are becoming increasingly fragmented. In North America, much attention has focused on fragmentation of forested habitat, particularly where there has been permanent forest loss due to agricultural and urban expansion. Although recurrent negative impacts, such as some edge effects, increased predation and herbivory, and failure of metapopulation dynamics, have been identified (Simberloff 1994), there have been few studies of fragmentation in managed landscapes where

patches of older forest are surrounded by regenerating forest (McGarigal and McComb 1995, Hagan et al. 1996).

Both the theory of island biogeography (MacArthur and Wilson 1963, 1967) and metapopulation theory (Levins 1970) predict species loss from habitat fragments, because of higher extinction and lower recolonization probabilities in isolated habitats. Island biogeography theory also predicts that extinction probability will vary inversely, and recolonization directly, with island area, and that species–area curves from fragmented habitats will have steeper slopes and lower intercepts than curves from continuous habitat. Metapopulation theory places greater emphasis on the role of the intervening matrix in mediating these rates. Connecting areas with corridors to facilitate movement among patches has been suggested many times as a

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conservation solution (e.g., Mann and Plummer 1993), but few empirical studies have supported this recommendation (Hobbs 1992, Simberloff et al. 1992). Although recent evidence suggests that birds use corridors for adult and juvenile dispersal (Haas 1995, Machtans et al. 1996), whether this reduces species loss in adjoining habitat fragments is not known.

The boreal forest is the most extensive forest ecosystem in North America, and probably the least understood. The mixed-wood region of the boreal forest in Canada extends from northeastern British Columbia into southern portions of the Northwest Territories, and through Alberta and Saskatchewan into southwestern Manitoba (Rowe 1972). Until recently, the boreal mixed-wood remained in a relatively natural state, where large, natural disturbances, such as fire and insect outbreaks, and smaller scale disturbances, such as treefalls, created a mosaic of stand types and successional stages. This naturally patchy habitat has one of the highest levels of bird species diversity in North America (Robbins et al. 1986). However, increasing pressure from industrial forestry is resulting in widespread habitat fragmentation and changes in forest composition (Schmiegelow and Hannon 1993). Older forests are being harvested first, and the structural and compositional complexity of these areas has been correlated with high species diversity and specialization (Stelfox 1995), leading to predictable conflicts between timber production and habitat conservation (Cumming et al. 1994).

The goal of our analyses was to estimate the severity of fragmentation effects on breeding boreal bird communities in old, mixed stands. We present the results from a replicated experiment in which boreal forest was harvested to leave older forest fragments of different sizes: some completely isolated and some connected by riparian buffer strips. We used birds to monitor the effects of fragmentation because they are relatively easy to census, have known sensitivities to habitat fragmentation elsewhere, and are good biological indicators for this system (see Schmiegelow and Hannon 1993). We tested the following predictions:

- 1) Species loss from fragmented areas will result in species–area curves with steeper slopes and lower intercepts relative to similar-sized areas within continuous forest.
- 2) Small fragments, in particular, will experience higher species turnover than large fragments, and will lose old-forest specialists and area-sensitive species.
- 3) Abundances of certain species will temporarily increase in recently fragmented areas, because of displacement of individuals from adjacent harvested areas.
- 4) Bird communities in connected fragments will be less affected by adjacent harvesting than will those in completely isolated fragments.

STUDY AREA

We conducted this research near Calling Lake, in north-central Alberta, Canada (55° N, 113° W). Our study area encompassed ≈140 km² of boreal mixed-wood forest, within the moist mixed-wood subregion. Trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*) are the most abundant upland tree species in this region, often occurring together in old, mixed stands, whereas black spruce (*Picea mariana*) characterizes wetter sites (Strong and Leggat 1981). The dominant understory shrubs are alder species (*Alnus tenuifolia*, *A. crispa*), with lesser amounts of willow (*Salix* spp.). Various fruiting shrubs (*Rubus*, *Ribes*, *Rosa* spp.), sarsaparilla (*Aralia nudicaulis*), and other herbaceous plants dominate the lower strata.

Mean summer (early June through mid-August) precipitation in the region is ≈320 mm, accounting for >70% of the total yearly precipitation; July is generally the wettest month. The mean summer temperature is 12.0°C, and the mean freeze-free period is 85 d (Strong and Leggat 1981).

METHODS

Experimental design

Our design involved two treatments: isolated and connected forest fragments, with common controls. Isolates were created by clear-cut logging a 200 m wide strip around forest patches. Connected patches of forest were isolated by 200 m of clear-cutting on three sides, with the fourth side connected to 100 m wide riparian buffer strips (Fig. 1). Isolated forest fragments were 1, 10, 40, and 100 ha in size; connected fragments were 1, 10, and 40 ha in size. We did not include any 100-ha connected fragments because sufficient, suitable forest adjacent to riparian areas was not available. Controls were placed within ≈4000 ha of continuous, adjacent forest. Each size class was replicated three times, within each treatment and control, as suggested by a priori power analyses (Schmiegelow and Hannon 1993).

We used forest inventory information and extensive ground-truthing to identify candidate study sites and to establish permanent sampling stations in 1992. All sites were in old (80–130 yr-old), aspen-dominated forest, similar in canopy height, canopy closure, tree species composition, and understory features. Variation in these features was stratified across replicate groups and size classes, within treatments and controls. For example, replicates in group 1 occurred in the youngest forest (80–100 yr old); replicates in group 2 were in older, relatively pure aspen forest (90–130 yr old), and replicates in group 3 were in older aspen forest (90–130 yr old) with some white spruce in the canopy. Each replicate group was represented by one site in each size class, in each treatment or control. This design allowed us to separate the effects of fragment area and of various attributes of habitat on the bird community.

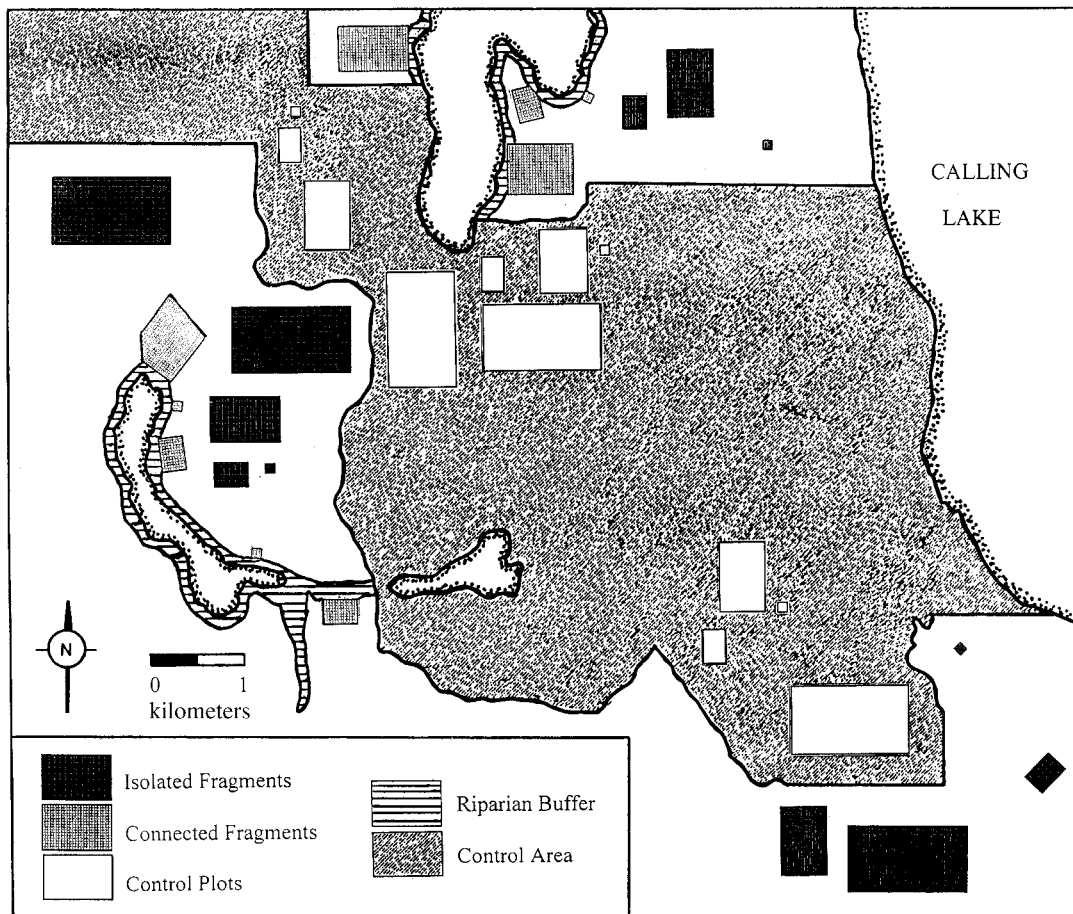


FIG. 1. Experimental layout of the Calling Lake Fragmentation Study (after Schmiegelow and Hannon 1993).

Prefragmentation data were collected in 1993 and the study area was harvested in the winter of 1993–1994, between November and March, according to the experimental design (Fig. 2). Two years of postfragmentation data (1994 and 1995) were collected.

Bird sampling

Permanent sampling stations were spaced at 200-m intervals, along transects 200 m apart, with the exception of 2–40 ha connected fragments, where sampling stations were spaced at 180-m intervals due to anomalies in the shape of these sites. Sampling intensity was proportional to area: 1-ha sites had one station, 10-ha sites had two, 40-ha sites had eight, and 100-ha sites had 20 stations, resulting in a total of 219 stations. In the 1-ha sites, a 50-m sampling radius was used because of area constraints; a 100-m sampling radius was used in all other sites. All comparisons we made were either before/after on the same sites, or between treatments and controls in the same size classes; thus, variation in sampling radius between size classes did not bias the analyses. Point count surveys were conducted at each station five times during the breeding season, at

10-d intervals, from the third week in May through late June each year. Upon arrival at a station, observers would wait for 1 min and would then record all individual birds seen and heard during a 5-min sampling interval, within 50-m and 100-m distance classes. All records at each station were mapped and movements were noted, ensuring that individuals were recorded only once per visit (see Ralph et al. 1993). Care was also taken, both in the field and when compiling data, to avoid recording the same individual at adjacent stations. Any additional behavioral observations, such as an adult carrying nesting material (see Table 1), were also recorded on the data cards.

All surveys were conducted between sunrise and 1000 in the morning, following general standards established by Ralph et al. (1993). Surveys were not conducted if it was raining, nor if estimated wind speed exceeded 25 km/h (Beaufort level 5; small branches move). The order in which we sampled size classes within replicate groups and treatments was standardized within each survey by sampling treatment and control areas in the same replicate group, in the same order, on the same day. Observer and diurnal variation

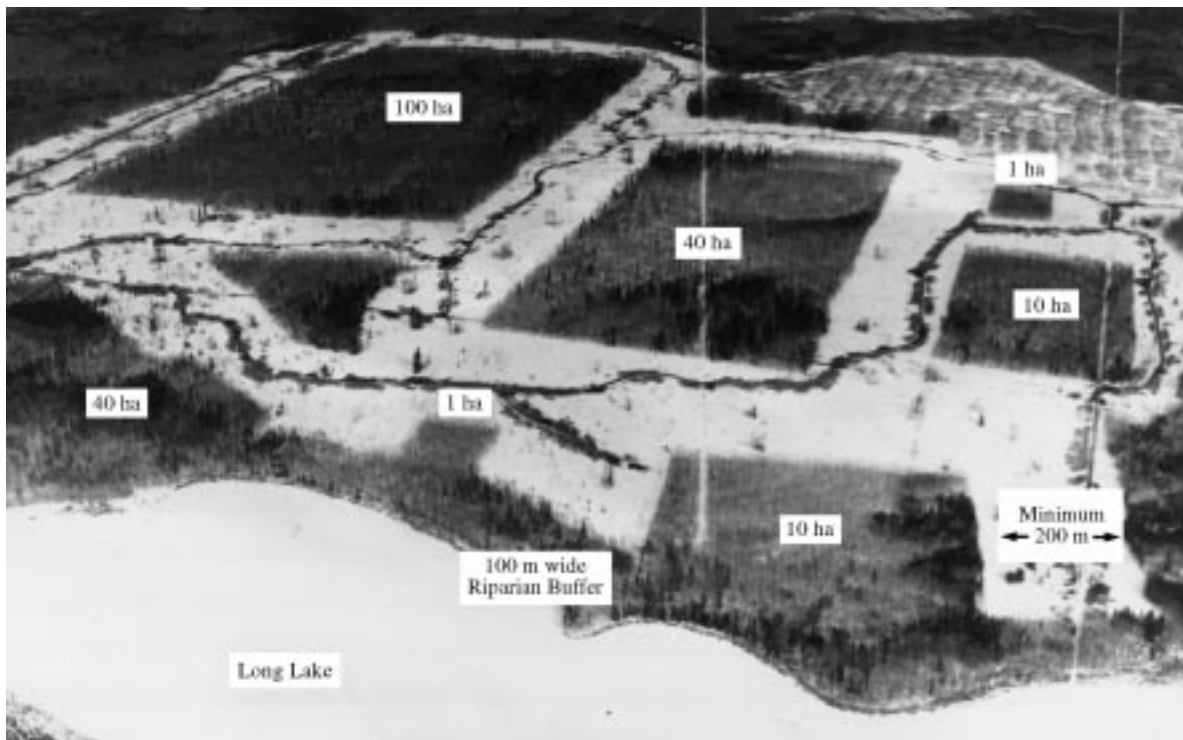


FIG. 2. Aerial view of a portion of the study area in November 1993, shortly after harvest. In the foreground is one set of connected fragments; in the background, one set of isolated fragments. Vertical straight lines are seismic exploration lines; irregular dark lines in harvested areas are haul roads with cut timber alongside.

were standardized across all stations, within each year, by rotating observers among study areas and varying the order in which stations in a given area were sampled. Eight observers conducted point counts in each year, and each round of counts took 2–3 days. Three observers were present in all three years, and an additional three participated in surveys in two of the three years.

Vegetation sampling

Detailed vegetation data were collected mid-July through early August at all stations, using a protocol modified from the BBIRD Program (Martin 1992a). At each station, four 0.04-ha plots were sampled; one cen-

tered on the station and three centered 40 m away at 0°, 120°, and 240°. Within each plot, ground cover in six categories (all green, forb, shrub, grass, leaf litter, moss) was estimated to the nearest 5% in four 1-m² quadrats; litter depth was measured at four locations; number of stems of shrubs (by species) was recorded for five 1-m² quadrats. Numbers of saplings (diameter at breast height, dbh <2.5 cm) and poles (2.5–8 cm dbh) of each species were counted in a 0.008-ha nested subplot. The number of trees of each species in four diameter classes (8–15, 15–23, 23–38, and >38 cm dbh), was recorded for the entire plot. We also recorded the species, dbh, and height of every snag >12 cm dbh, and the total number of snags <12 cm dbh. We used clinometers to measure average canopy, subcanopy, and tall shrub height, and measured canopy closure as the mean of four densiometer readings per plot.

TABLE 1. Abundance weightings for bird observations.

| Behavior | Weight† | No. detections‡ |
|------------------------------------|---------|-----------------|
| Singing or countersinging male | 1.0 | 19 885 |
| Calling or observed male or female | 0.5 | 1598 |
| Territorial dispute | 1.0 | 8 |
| Pair observed | 2.0 | 146 |
| Active nest observed | 2.0 | 23 |
| Juvenile observed | 2.0 | 15 |
| Adult carrying nesting material | 2.0 | 14 |
| Adult carrying food | 2.0 | 17 |
| Distraction display | 2.0 | 2 |

† Mean weighting factor = 0.98.

‡ Total no. detections = 21 340.

Data analyses

Prior to analysis, all data sets were tested for normality using a Shapiro-Wilks test, and for homogeneity of variance with the Levene statistic (Conover 1980, Norusis 1993). Where possible, data were transformed to satisfy the assumptions of parametric statistical tests. When assumptions could not be satisfied, nonparametric tests were used. When analyzing vegetation data, we used an alpha level of 0.05, because of large sample sizes and associated high power. When inter-

TABLE 2. Summary of vegetation variables and results of analyses of data collected at Calling Lake, Alberta, Canada, 1993–1995.

| Variable† | Controls | Isolated fragments | Connected fragments | F ratio | P |
|--|----------|--------------------|---------------------|----------|--------|
| Percent cover | | | | | |
| All green | 52.21 | 53.45 | 50.49 | 1.023 | 0.361 |
| Grass§ | 7.55 | 7.17 | 2.72 | 13.171 | <0.001 |
| Shrubs | 25.21 | 27.10 | 22.36 | 2.740 | 0.067 |
| Leaf litter | 71.37 | 73.38 | 79.82 | (4.019) | 0.134 |
| Moss§ | 3.92 | 5.43 | 5.59 | 1.526 | 0.220 |
| Counts | | | | | |
| Deciduous stems (no.) | 118.14 | 111.58 | 102.79 | (2.892) | 0.058 |
| Deciduous basal area (m ²) | 3.80 | 3.64 | 3.84 | 0.566 | 0.569 |
| Mesic coniferous stems (no.) | 14.66 | 9.83 | 11.48 | 0.927 | 0.397 |
| Hygic coniferous stems (no.)§ | 2.82 | 5.54 | 6.33 | 0.444 | 0.642 |
| Coniferous basal area§ (m ²) | 0.51 | 0.36 | 0.58 | 2.676 | 0.071 |
| Deciduous saplings (no.) | 142.91 | 101.10 | 76.52 | (15.971) | <0.001 |
| Coniferous saplings (no.)§ | 3.03 | 2.23 | 1.24 | 4.037 | 0.019 |
| Shrub stems (no.) | 95.56 | 93.46 | 88.67 | 0.453 | 0.636 |
| Large snags (no.) | 16.34 | 14.75 | 13.36 | 1.491 | 0.228 |
| Snag basal area (m ²) | 0.21 | 0.21 | 0.15 | 2.862 | 0.059 |
| Average snag height (m) | 9.87 | 9.76 | 9.34 | 0.163 | 0.849 |
| Physical descriptors | | | | | |
| Canopy height (m) | 27.63 | 27.23 | 27.08 | 0.301 | 0.741 |
| Subcanopy height (m) | 13.84 | 13.50 | 14.12 | 0.336 | 0.715 |
| Tall shrub layer height (m) | 3.57 | 4.08 | 3.57 | 4.716 | 0.010 |
| Canopy closure (m ²) | 77.83 | 73.75 | 74.76 | (9.385) | 0.009 |

† All variable values are averages of data at the point-count station level.

‡ All F ratios were calculated using a one-way ANOVA, except for values in parentheses, which are χ^2 statistics from a Kruskal-Wallis nonparametric ANOVA. For all tests, $n = 93$ for controls and isolated fragments and $n = 33$ for connected fragments; $df = 2, 216$.

§ Data were $\log(x + 1)$ -transformed prior to statistical analyses. Nontransformed data are reported in the table.

preting the results of statistical tests on bird community measures, we used an alpha level of 0.10, because we feel that Type II errors can be more costly than Type I errors in applied research (see Peterman 1990, Schmiegelow 1992, Smith 1995). We used the Bonferroni correction for multiple comparisons where appropriate (Winer et al. 1991).

Relative sampling area, rather than study site area, was used in all regression and ANOVA models. For 1-ha sites, sampled area (one station with a 50-m sampling radius) was considered equivalent to actual area, and other sites were scaled accordingly (e.g., a 10-ha site with two stations, each with a sampling radius of 100 m, has a sampled area eight times that of a 1-ha site).

Vegetation patterns.—The original vegetation data set contained >100 variables. Initially, we used two-dimensional principal component analysis (PCA) to reduce the data set. However, the PCA factors did not adequately explain the variation in the data (broken stick criteria; Legendre and Legendre 1983), so a subset of actual variables was chosen for analysis. We used 20 variables that either had high factor loadings, or that summarized the obvious gradients on the PCA plots. For example (see Table 2), a site–moisture gradient was represented by hygic conifers (larch, *Larix laricina*; black spruce) and mesic conifers (jack pine, *Pinus banksiana*; white spruce).

We used one-way ANOVAs to determine if the mean values of each variable differed between our treatment and control areas, because the data did not satisfy the assumptions necessary for MANOVA (Maxwell and Delaney 1990). We $\log(x + 1)$ -transformed variables that were markedly non-normally distributed, and used a Kruskal-Wallis nonparametric ANOVA for variables that were not homoscedastic between sites.

Description of the bird community.—Although we recorded all bird species seen or heard during point count surveys, we removed all raptors, corvids, shorebirds, waterfowl, and grouse prior to analyses, since our methods did not sample such species adequately. We also removed all woodpeckers except the Yellow-bellied Sapsucker (scientific names in Appendix). The Yellow-bellied Sapsucker is the only nonresident woodpecker that occurs in significant numbers in our study sites. Because this species breeds later, and is much more conspicuous than resident woodpeckers in the area, it is better suited to the sampling methods we used. To standardize sampling area and confirm site occupancy, we did not include any individuals that were only recorded flying over or through the forest during point counts.

Bird species richness.—We generated two species richness estimates for each of our study sites in each year. One excluded the first round of point counts, conducted during the third week of May, owing to the high

frequency of late migrants during this period. It otherwise included all species records, and is herein referred to as "all species." Unless noted, all analyses were done using "all species." The second estimate was based on information from all rounds, but included only species for which there was evidence of probable or confirmed breeding, following standards similar to those used by breeding-bird atlas projects (e.g., Semenchuck 1992). We used the following criteria, assessed at each station: singing male heard on more than one occasion (i.e., ≥ 10 d apart); pair, juvenile, or family group observed; individual observed carrying nesting material or food, or performing a distraction display. We refer to this group of species as "probable breeders only" (see also Opdam et al. 1985, Hinsley et al. 1995).

Species richness and area measures were log-transformed to generate species-area curves for each treatment and for the controls, in each year. Linear regression was used to quantify species-area relationships. We tested for differences between years within treatment and control groups using repeated-measures analysis of covariance (RM ANCOVA), and for within-year differences between groups (independent observations) using ANCOVA.

Measures of diversity and similarity.—We used abundance curves to characterize overall community structure (May 1975, Southwood 1978) and to select an appropriate diversity index (Magurran 1988). We pooled data for all species across all treatments and years for this purpose (Appendix). We first generated a rank abundance plot (Whittaker 1965), and then generated a frequency distribution of species abundances, plotting number of species against number of individuals per species (\log_2 classes, or octaves), after Preston (1948). Inspection of these curves suggested that the data were best represented by the logarithmic series (Fisher et al. 1943). We also generated rank abundance curves for treatment and control groups, in each year, to check for fits to different models, because we wished to compare communities with a common diversity index. All species abundance distributions suggested that the most appropriate diversity index for our data was the log series alpha (α) (Williams 1964, after Fisher et al. 1943).

Calculation of α values requires two variables: the total number of species in the sample (S) and the total number of individuals (N). Through iterative solution of Eq. 1, we obtained values for x , the parameter of the logarithmic series, and then solved Eq. 2 to obtain α values for each station and site, in each year:

$$\frac{S}{N} = \frac{(1-x)}{x(-\ln[1-x])} \quad (1)$$

$$\alpha = \frac{N(1-x)}{x} \quad (2)$$

The log series index shows good discriminant ability

in a wide range of circumstances (Southwood 1978), and low sensitivity to variation in sample size (Taylor et al. 1976, Taylor 1978). Taylor (1978) promotes α as a good measure of diversity even when the underlying species abundances do not exhibit a log series distribution. Further, it is less affected by species dominance than are the more widely used Shannon or Simpson indices (Magurran 1988). An additional feature of this index is that it provides an alternative to rarefaction for detecting sampling artifacts due to unequal sample sizes, as may be the case with some species-area relationships (e.g., Freemark and Merriam 1986), but it preserves more information (Rosenzweig 1995).

We used the Jaccard coefficient (J) to quantify similarity of sites between years. We used this index because it excludes species absent in both samples (see also Krebs 1989) and because it is less sensitive to variation in sample size and species richness than are other indices (Wolda 1981). We defined percentage turnover as $(1 - J) \times 100$.

Bird abundance.—All observations were weighted according to evidence of breeding (Table 1). Although it is common to assign a weighting of 2 to singing males, assuming that a singing male represents a pair (e.g., Helle 1984, Lynch and Whigham 1984), we chose not to do this for two reasons. First, most detections during point count surveys are of singing males, resulting in a mean weighting factor that exceeds 1, and thereby artificially inflating the sample. Second, a possible outcome of habitat fragmentation is an increase in the number of unpaired males (Gibbs and Faaborg 1990, Villard et al. 1993). We also had two reasons for using mean abundance per sampling round, rather than maximum abundance in any round (e.g., Welsh and Lougheed 1996), as an estimate of the relative abundance of each species at each station in each year. Other authors have used the maximum number of birds, because point count data represent incomplete counts (Barker and Sauer 1995); in our case, however, this could bias results by exacerbating variation due to multiple observers, and by equally weighting nonterritorial or transient individuals.

We tested for treatment effects on individual species with more than five detections in any year in both treatments and controls by using simple contrasts, equivalent to the interaction term of a two-group repeated-measures ANOVA (von Ende 1993), to compare changes in abundance over the three study (years 1993–1995). Using G tests, we examined the proportion of species that declined after harvesting as a function of migration strategy.

RESULTS

Vegetation patterns

Prior to testing for experimental effects of area and isolation on the bird communities, we first determined whether or not our treatments and controls had com-

TABLE 3. Regression statistics for species–area relationships of forest birds in treatment and controls in 1993, 1994, and 1995 ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments, in each year).

| | Year | r^2 | P | z^\dagger | $SE(z)^\ddagger$ | c^\S | $SE(c)^\parallel$ |
|---------------------|------|-------|--------|-------------|------------------|--------|-------------------|
| All species | | | | | | | |
| Controls | 1993 | 0.90 | <0.001 | 0.42 | 0.042 | 0.76 | 0.052 |
| | 1994 | 0.81 | <0.001 | 0.39 | 0.056 | 0.76 | 0.070 |
| | 1995 | 0.88 | <0.001 | 0.38 | 0.043 | 0.84 | 0.054 |
| Isolated fragments | 1993 | 0.78 | <0.001 | 0.46 | 0.072 | 0.70 | 0.090 |
| | 1994 | 0.79 | <0.001 | 0.42 | 0.065 | 0.75 | 0.081 |
| | 1995 | 0.74 | <0.001 | 0.44 | 0.077 | 0.74 | 0.096 |
| Connected fragments | 1993 | 0.72 | 0.002 | 0.40 | 0.086 | 0.87 | 0.080 |
| | 1994 | 0.81 | <0.001 | 0.44 | 0.075 | 0.78 | 0.070 |
| | 1995 | 0.74 | 0.002 | 0.25 | 0.051 | 1.02 | 0.048 |
| Probable breeders | | | | | | | |
| Controls | 1993 | 0.84 | <0.001 | 0.42 | 0.056 | 0.53 | 0.070 |
| | 1994 | 0.81 | <0.001 | 0.52 | 0.075 | 0.37 | 0.093 |
| | 1995 | 0.86 | <0.001 | 0.44 | 0.054 | 0.51 | 0.067 |
| Isolated fragments | 1993 | 0.86 | <0.001 | 0.43 | 0.052 | 0.55 | 0.066 |
| | 1994 | 0.75 | <0.001 | 0.40 | 0.068 | 0.60 | 0.085 |
| | 1995 | 0.69 | <0.001 | 0.44 | 0.087 | 0.49 | 0.108 |
| Connected fragments | 1993 | 0.67 | 0.004 | 0.47 | 0.114 | 0.55 | 0.107 |
| | 1994 | 0.78 | 0.001 | 0.42 | 0.078 | 0.60 | 0.073 |
| | 1995 | 0.75 | 0.002 | 0.37 | 0.075 | 0.62 | 0.070 |

† Slope estimate.

‡ Standard error of slope estimate.

§ Intercept estimate.

$^\parallel$ Standard error of intercept estimate.

parable vegetative attributes. Most of the variables used to describe vegetation structure were similar between treatment and control areas ($P \geq 0.003$; $df = 2, 216$ with Bonferroni correction; Table 2). Mean percent cover of grass was 5% lower in the connected fragments, a difference we do not consider biologically significant. The density of deciduous saplings (with an average of 33.0% *Alnus* spp.) also differed between our treatments and controls; these form a tall shrub layer that is an important structural feature of habitats in our study area. *Alnus* density is highly positively correlated with both average yearly abundance and species richness of birds in all three sites ($P \leq 0.006$). However, when we included density of deciduous saplings as a covariate for all tests in the prefragmentation year, we found that its effect was negligible, so we removed it from subsequent analyses.

Bird community

We analyzed data from 58 passerine species and the Yellow-bellied Sapsucker (Appendix). Neotropical migrant species form the largest component of the community in old, aspen-dominated stands, with 32 species

accounting for 63.7% of all records. Short-distance migrants are second in overall dominance, with 22 species representing 30.1% of records; the five resident species included in these analyses account for the remaining 6.2% of records. We also recorded five additional woodpecker species (Downy Woodpecker, *Picoides pubescens*; Hairy Woodpecker, *Picoides villosus*; Three-toed Woodpecker, *Picoides tridactylus*, Black-backed Woodpecker, *Picoides arcticus*; and Pileated Woodpecker, *Dryocopus pileatus*), and five species of corvids (Gray Jay, *Perisoreus canadensis*; Blue Jay, *Cyanocitta cristata*; Black-billed Magpie, *Pica pica*; American Crow, *Corvus brachyrhynchos*; and Common Raven, *Corvus corax*), all residents, over the 3-yr course of this study.

Species–area relationships.—All species–area regressions were significant, with area explaining a large proportion of the variation in species number across both treatment and control areas (Table 3), as would be expected from our study design. There were no significant changes in either the slope or intercept of these relationships within the controls, isolated fragments, or connected fragments during the three years of this study (1993–1995; Table 4). There were also no significant

TABLE 4. Repeated-measures ANCOVA results for species–area relationships of forest birds within treatment and control areas 1993–1995 ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments, in each year).

| | All species | | | | Probable breeders only | | | |
|---------------------|-------------|-------|-------|-------|------------------------|-------|-------|-------|
| | F ratio | df | Alpha | Beta | F ratio | df | Alpha | Beta |
| Controls | 2.55 | 2, 22 | 0.101 | 0.405 | 2.35 | 2, 22 | 0.118 | 0.437 |
| Isolated fragments | 0.06 | 2, 22 | 0.942 | 0.885 | 1.33 | 2, 22 | 0.285 | 0.623 |
| Connected fragments | 1.99 | 2, 16 | 0.169 | 0.511 | 0.05 | 2, 16 | 0.950 | 0.888 |

TABLE 5. ANCOVA results for comparison of species–area relationships for forest birds between treatment and control areas ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments).

| | Slope† | | | Intercept‡ | | |
|-------------------------|----------------|-------|-------|----------------|-------|-------|
| | <i>F</i> ratio | Alpha | Beta | <i>F</i> ratio | Alpha | Beta |
| All species | | | | | | |
| Prefragmentation (1993) | 0.24 | 0.787 | 0.845 | 1.51 | 0.239 | 0.581 |
| 1 yr postfragmentation | 0.12 | 0.888 | 0.872 | 0.45 | 0.643 | 0.801 |
| 2 yr postfragmentation | 1.89 | 0.171 | 0.509 | 1.69 | 0.203 | 0.546 |
| Probable breeders only | | | | | | |
| Prefragmentation (1993) | 0.11 | 0.896 | 0.874 | 0.29 | 0.752 | 0.834 |
| 1 yr postfragmentation | 0.87 | 0.431 | 0.714 | 2.01 | 0.152 | 0.486 |
| 2 yr postfragmentation | 0.21 | 0.881 | 0.851 | 0.65 | 0.528 | 0.758 |

† $df = 2, 30$.‡ $df = 2, 29$.

changes in the relationships among controls, isolated fragments, and connected fragments over the same time period (Table 5, Fig. 3). These results are contrary to our first prediction.

The only significant change in species richness occurred in the 1-ha connected fragments, where the number of species in 1995 (two years postfragmentation) increased relative to 1993 and 1994 (Friedman's $\chi^2 = 4.67$, $P = 0.097$, $df = 2$). These small, connected fragments also contained more species in 1995 than did equally sized isolated fragments and controls ($F = 4.047$; $df = 2, 6$; $P = 0.077$). However, the number of species considered to be probable breeders in the 1-ha connected fragments did not change significantly ($\chi^2 = 0.86$, $P = 0.649$), suggesting that the increase was due to transient species.

Species diversity.—There was no significant relationship between α diversity, as measured by the log series index, and area in the controls or treatments prior to fragmentation (1993) (Pearson's correlation coefficient: $r = 0.22$ to 0.40 , $P = 0.203$ to 0.557 ; Fig. 4A), suggesting that the observed species–area relationships were an artifact of sample size (see *Discussion*). There remained no significant relationship in either the controls or connected fragments for the two years after fragmentation ($r = -0.04$ to 0.34 , $P = 0.365$ to 0.950). However, the relationship was significant in both years following fragmentation for the isolated fragments (regression: $F = 12.99$; $df = 1, 10$; $P_{1994} = 0.005$, $R^2 = 0.565$; $F = 12.80$; $df = 1, 10$; $P_{1995} = 0.005$, $R^2 = 0.561$; Fig. 4B, C), due primarily to a decrease in diversity in the 1-ha and 10-ha isolates, revealing the occurrence of a true species–area relationship in these sites.

Species turnover.—We found significant differences in the composition of species supported by sites before and after fragmentation ($F = 2.94$; $df = 2, 30$; $P = 0.069$; Fig. 5). Isolated fragments were less similar overall (they had higher species turnover) than either control sites ($F = 4.11$; $df = 1, 22$; $P = 0.055$) or connected fragments ($F = 5.68$; $df = 1, 19$; $P = 0.029$), which did not differ in their similarity ($F = 0.01$; df

$= 1, 19$; $P = 0.943$). This effect was most pronounced in small isolates, consistent with our second prediction, and for resident species. Turnover averaged 92.6% in the 1-ha isolated fragments, compared with 71.0% and 66.3% in the 1-ha connected fragments and controls, respectively. Prior to fragmentation, there were five records of resident species, including the Black-capped Chickadee, Brown Creeper, and Red-breasted Nuthatch, in the three 10-ha isolates; however, there were none two years after fragmentation. When only probable breeders were considered, there was no significant difference in species turnover between treatments and controls ($F = 0.52$; $df = 2, 30$; $P = 0.597$); however, rates in the 1-ha isolated and connected fragments (94.4%, both cases) were high relative to the controls (75%), as reflected in the similarity–area curves with steeper slopes.

Bird abundance.—There was no significant difference in total abundance of all species in the controls or treatments prior to fragmentation ($F = 0.38$; $df = 2, 216$; $P = 0.683$; Fig. 6A). More individuals were recorded in the isolated fragments than in either the controls or connected fragments one year after fragmentation ($F = 8.43$; $df = 2, 216$; $P < 0.001$), but differences were not significant two years after fragmentation ($F = 1.57$; $df = 2, 216$; $P = 0.207$; Fig. 6A), supporting our third prediction concerning temporary crowding effects in the recently fragmented areas. Abundance trends did, however, differ among migratory groups.

Prior to fragmentation, numbers of Neotropical migrants (NTM) and short-distance (SD) migrants did not differ among treatments and controls ($F_{NTM} = 1.86$; $df = 2, 216$; $P_{NTM} = 0.156$, Fig. 6B; $F_{SD} = 0.61$; $df = 2, 216$; $P_{SD} = 0.542$, Fig. 6C), although resident (RES) numbers were lower in connected fragments ($F = 2.49$; $df = 2, 216$; $P = 0.087$, Fig. 6D). Neotropical migrant numbers increased in the isolated fragments relative to the controls, but not in the connected fragments, immediately following fragmentation ($F = 5.95$; $df = 2, 216$; $P = 0.003$, Bonferroni correction). Two years after fragmentation, however, both isolated and connected

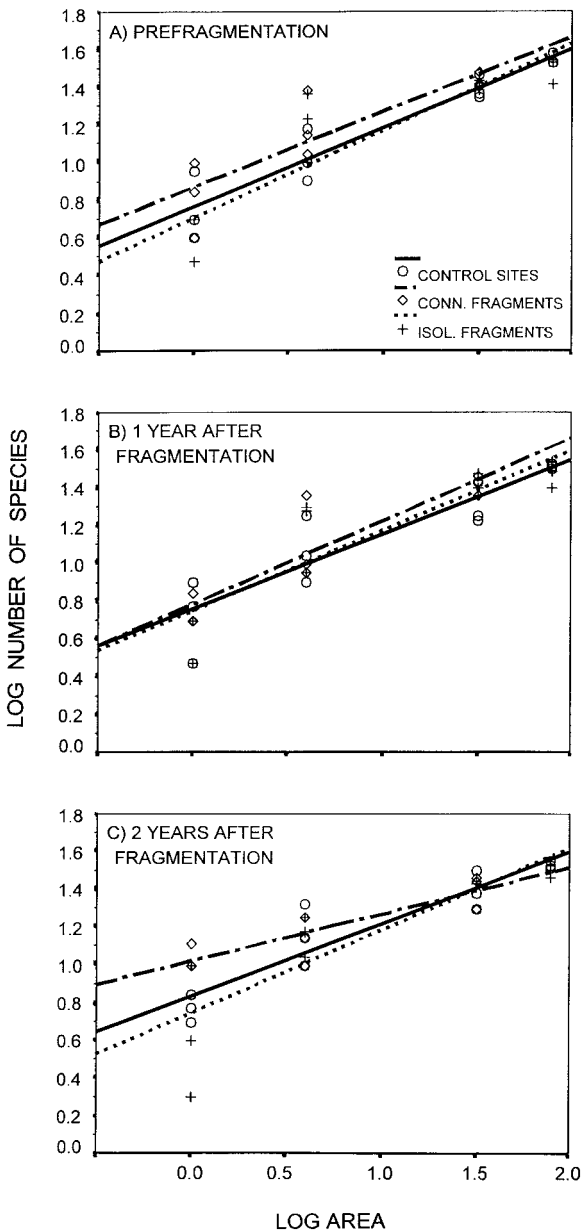


FIG. 3. Species-area curves for forest birds ("all species") in treatment and control areas (A) before fragmentation, (B) one year after fragmentation, and (C) two years after fragmentation ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments).

fragments contained fewer Neotropical migrants than did control sites ($F = 6.50$; $df = 2, 216$; $P = 0.002$, Bonferroni correction; Fig. 6B). Numbers of short-distance migrants were significantly higher in the isolated fragments than in connected fragments, but not higher than in controls, immediately after fragmentation ($F = 6.25$; $df = 2, 216$; $P = 0.002$, Bonferroni correction). They did not differ among treatments and controls in the second year ($F = 2.04$; $df = 2, 216$; $P = 0.130$; Fig. 6C). Abundance of resident species remained lowest

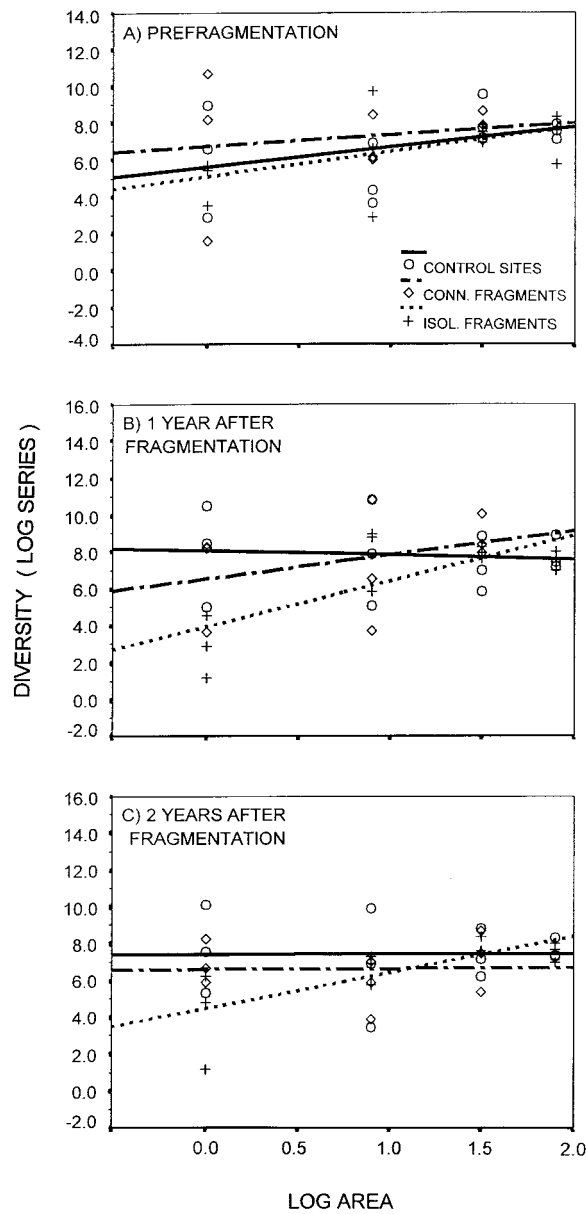


FIG. 4. Log series α diversity of forest birds in treatment and control areas (A) before fragmentation, (B) one year after fragmentation, and (C) two years after fragmentation. The only significant regressions were for the isolated fragments in (B) and (C) ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments).

in the connected fragments one year following fragmentation ($F = 3.52$; $df = 2, 216$; $P = 0.031$, Bonferroni correction). In the second year, resident numbers were lower in both the isolated and connected fragments than in the controls, and isolated and connected fragments were no longer significantly different ($F = 15.68$; $df = 2, 216$; $P < 0.001$, Bonferroni correction; Fig. 6D).

We had sufficient observations (more than five in any year in both treatments and controls) to analyze data from 37 species in isolated fragments and 30 spe-

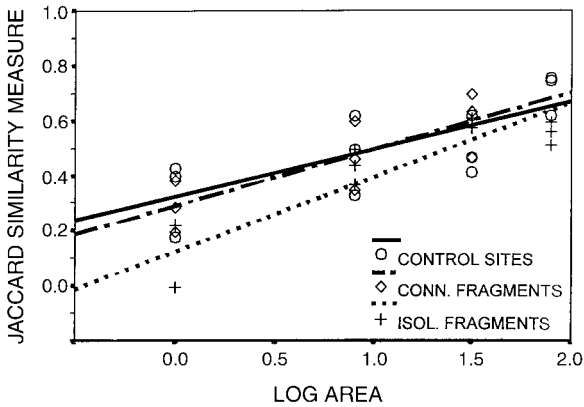


FIG. 5. Similarity of bird species assemblages within treatment and control areas from prefragmentation (1993) to two years after fragmentation (1995) ($n = 12$ for controls and isolated fragments and $n = 9$ for connected fragments).

fect on seven species in the isolated fragments and six species in the connected fragments, and a significant positive effect on three species in the isolated and two species in the connected fragments (Table 7). Five of the seven species that declined due to fragmentation in the isolated fragments were Neotropical migrants and the remaining two species were residents, a significantly nonrandom distribution with respect to overall community composition ($G = 6.40, P = 0.041$). All of the species negatively affected in the connected fragments were Neotropical migrants, also significantly nonrandom ($G = 4.86, P = 0.088$). There was no significant pattern with respect to migratory habit in the species positively affected by fragmentation in either the isolated ($G_I = 1.98, P_I = 0.372$) or connected fragments ($G_C = 0.82, P_C = 0.664$).

cies in connected fragments, comparing changes in individual species abundances over the 3-yr course of this study (1993–1995) relative to changes observed in our controls (Table 6). Measured two years after forest harvesting, fragmentation had a significant negative ef-

When only trends from before fragmentation to one year after fragmentation were considered (1993–1994), many of the species that declined significantly over the longer term in the isolated fragments exhibited increases, consistent with our crowding hypothesis (Table 6). These species included the Black-throated Green Warbler, Chipping Sparrow, Rose-breasted Grosbeak, and Ruby-crowned Kinglet. This pattern was not apparent in the connected fragments.

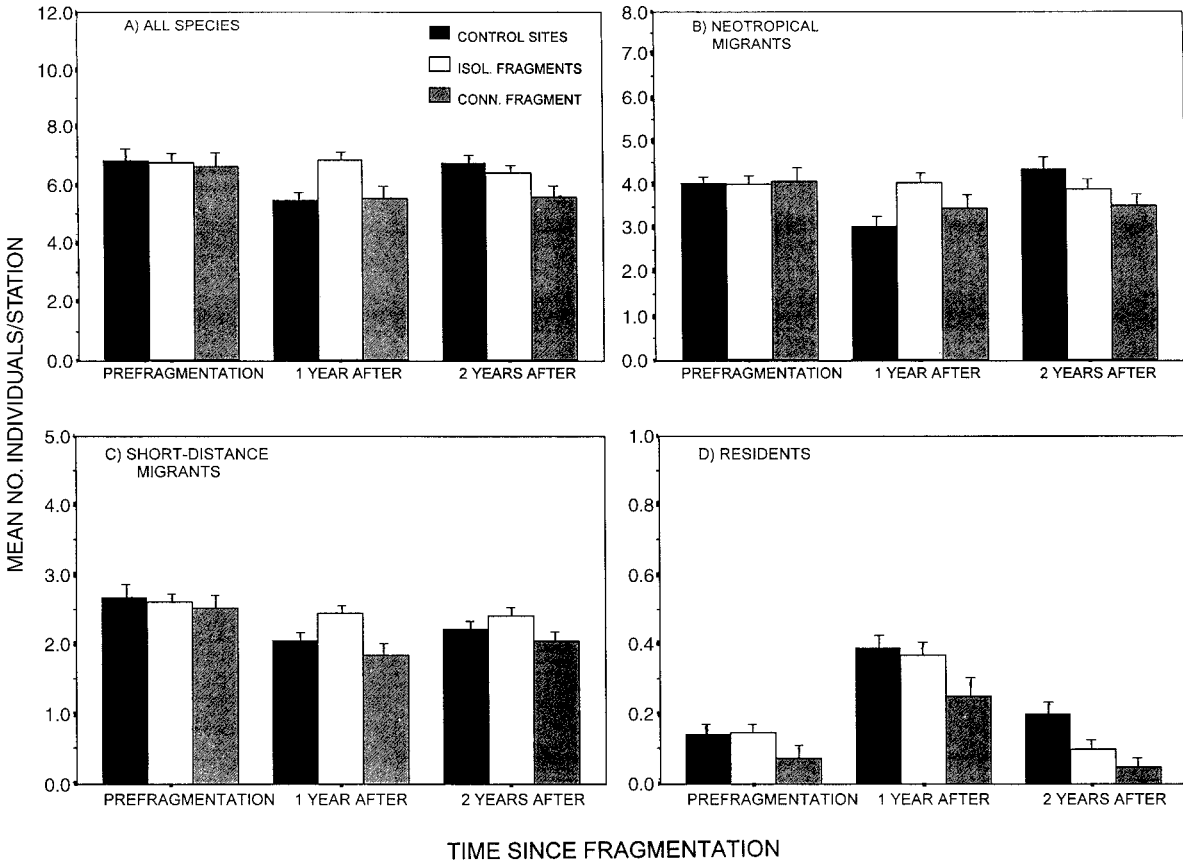


FIG. 6. Changes in mean (± 1 SE) relative abundance per sampling station within and between treatment and control areas for (A) all bird species, (B) Neotropical migrants, (C) short-distance migrants, and (D) resident species ($n = 93$ for controls and isolated fragments and $n = 33$ for connected fragments).

TABLE 6. Total relative abundances of bird species in both treatments and controls before fragmentation (1993), and in the two years following fragmentation (1994 and 1995). Abundance weightings are in Table 1. Species are listed from most to least abundant within migration categories ($n = 93$ sampling stations for controls and isolated fragments; $n = 33$ for connected fragments).

| Species | Controls | | | Isolated fragments | | | Connected fragments | | |
|--------------------------------|----------|-------|-------|--------------------|-------|-------|---------------------|-------|-------|
| | 1993 | 1994 | 1995 | 1993 | 1994 | 1995 | 1993 | 1994 | 1995 |
| Neotropical migrants | | | | | | | | | |
| Ovenbird | 439.0 | 247.0 | 311.0 | 296.5 | 208.5 | 141.0 | 156.0 | 99.5 | 63.5 |
| Red-eyed Vireo | 221.5 | 177.0 | 236.0 | 165.0 | 194.5 | 173.0 | 65.0 | 89.0 | 97.5 |
| Least Flycatcher | 161.5 | 166.5 | 167.5 | 222.5 | 248.0 | 253.5 | 62.5 | 53.5 | 75.5 |
| Black-throated Green Warbler | 220.0 | 147.5 | 167.5 | 230.5 | 209.5 | 142.5 | 47.0 | 46.0 | 28.5 |
| Mourning Warbler | 141.0 | 142.5 | 144.0 | 162.0 | 209.0 | 210.0 | 39.0 | 54.0 | 43.0 |
| Tennessee Warbler | 17.5 | 35.0 | 294.0 | 37.0 | 43.0 | 224.0 | 4.0 | 6.0 | 50.0 |
| American Redstart | 91.5 | 79.0 | 74.5 | 146.5 | 146.0 | 120.5 | 20.5 | 20.5 | 7.0 |
| Connecticut Warbler | 78.0 | 73.0 | 74.0 | 113.0 | 131.0 | 99.5 | 47.0 | 37.0 | 50.0 |
| Yellow Warbler | 59.5 | 60.5 | 82.5 | 91.5 | 109.0 | 105.5 | 33.0 | 38.0 | 19.0 |
| Chipping Sparrow | 85.0 | 65.0 | 131.5 | 58.0 | 68.0 | 52.0 | 29.0 | 21.0 | 33.0 |
| Swainson's Thrush | 64.0 | 51.5 | 92.0 | 41.0 | 52.0 | 72.5 | 33.0 | 20.5 | 23.5 |
| Western Tanager | 81.0 | 47.0 | 48.5 | 53.0 | 68.0 | 42.0 | 32.5 | 32.5 | 26.5 |
| Rose-breasted Grosbeak | 34.0 | 26.5 | 74.5 | 65.0 | 66.0 | 58.5 | 33.5 | 16.0 | 13.0 |
| Warbling Vireo | 42.0 | 20.0 | 19.0 | 55.0 | 36.0 | 37.0 | 11.0 | 4.0 | 4.0 |
| Solitary Vireo | 46.0 | 35.0 | 20.0 | 29.5 | 24.0 | 21.0 | 15.0 | 12.0 | 9.0 |
| Lincoln's Sparrow | 26.5 | 15.0 | 7.0 | 27.0 | 15.0 | 7.0 | 6.0 | 3.0 | 0 |
| Ruby-crowned Kinglet | 16.0 | 3.0 | 22.0 | 17.0 | 9.0 | 7.0 | 18.0 | 2.0 | 11.0 |
| Philadelphia Vireo | 20.0 | 5.0 | 12.0 | 26.0 | 7.0 | 11.0 | 10.0 | 2.0 | 5.0 |
| Magnolia Warbler | 11.0 | 7.0 | 11.0 | 15.0 | 8.0 | 4.0 | | | |
| Western Wood Peewee | 13.5 | 12.0 | 4.0 | 1.0 | 0 | 6.0 | 2.0 | 1.0 | 7.0 |
| Canada Warbler | 0 | 0 | 5.0 | 1.0 | 1.0 | 5.5 | | | |
| Short-distance migrants | | | | | | | | | |
| White-throated Sparrow | 587.5 | 453.0 | 467.5 | 656.5 | 602.0 | 556.0 | 157.0 | 118.0 | 118.0 |
| Yellow-rumped Warbler | 360.0 | 311.5 | 365.5 | 302.5 | 338.0 | 368.0 | 145.0 | 89.5 | 140.5 |
| Yellow-bellied Sapsucker | 116.5 | 54.0 | 44.0 | 82.5 | 48.0 | 48.5 | 46.0 | 34.0 | 14.5 |
| Winter Wren | 46.0 | 32.0 | 75.0 | 38.0 | 50.0 | 59.0 | 19.0 | 15.0 | 33.0 |
| Brown-headed Cowbird | 29.5 | 17.0 | 15.5 | 15.0 | 25.5 | 12.0 | 18.5 | 15.5 | 12.5 |
| American Robin | 4.0 | 28.5 | 15.0 | 0 | 19.0 | 13.0 | 4.0 | 14.5 | 7.5 |
| Dark-eyed Junco | 17.0 | 18.0 | 10.0 | 20.5 | 11.5 | 11.0 | | | |
| Pine Siskin | 27.5 | 3.0 | 2.0 | 31.5 | 2.5 | 0 | 11.0 | 2.0 | 3.0 |
| Hermit Thrush | 7.5 | 10.0 | 11.0 | 8.0 | 7.0 | 24.0 | | | |
| Cedar Waxwing | 5.0 | 2.0 | 9.0 | 8.5 | 10.0 | 18.5 | | | |
| White-winged Crossbill | 20.0 | 1.0 | 0 | 24.5 | 1.0 | 0.5 | 6.0 | 0 | 0 |
| House Wren | 14.0 | 1.0 | 1.0 | 9.0 | 8.0 | 12.0 | | | |
| Purple Finch | 0 | 0 | 7.0 | 2.0 | 3.0 | 5.0 | | | |
| Residents | | | | | | | | | |
| Red-breasted Nuthatch | 11.0 | 100.5 | 27.5 | 15.0 | 106.5 | 6.5 | 3.0 | 23.0 | 5.5 |
| Brown Creeper | 27.5 | 52.5 | 35.0 | 12.5 | 41.0 | 14.0 | 3.0 | 10.0 | 1.0 |
| Black-capped Chickadee | 22.0 | 24.0 | 29.5 | 37.0 | 20.0 | 21.0 | 6.0 | 5.0 | 1.0 |

Note: Only species with more than five detections in any year in both treatments and controls are included.

DISCUSSION

We made four predictions concerning broad-scale responses of the avian community to experimental forest fragmentation: (1) that species loss from fragmented areas would result in species-area relationships with steeper slopes and lower intercepts; (2) that small fragments would experience high species turnover and would lose specialist species of older forest; (3) that abundances of some species would temporarily increase in recently created forest fragments, due to displacement of individuals from adjacent cut areas; and (4) that connected fragments would maintain their pre-fragmentation community structure better than would completely isolated fragments. Our results were consistent with predictions 2–4, but the magnitudes of the effects we observed were small compared with those

observed elsewhere. We observed no net loss of species from fragmented areas, although the log series α revealed changes in the species-area relationship of the isolated fragments when the influence of sample size was removed. We documented higher turnover rates and crowding effects immediately after fragmentation, as well as significant declines in the abundance of certain species in the second year following fragmentation, indicating that overall community structure had been altered. We also found some evidence that connections between fragments helped to offset these effects.

Species loss due to fragmentation

We found a significant relationship between number of species and area, and turnover of species in the com-

TABLE 7. Effect of treatment on bird species abundances in isolated and connected forest fragments one and two years after fragmentation. Species listings are as in Table 6.

| Species | Status [†] | Isolated fragments | | | | Connected fragments | | | |
|------------------------------|---------------------|---------------------|-----------------------|--------|----------|---------------------|----------|--------|----------|
| | | Year 1 | | Year 2 | | Year 1 | | Year 2 | |
| | | Effect [‡] | <i>P</i> [§] | Effect | <i>P</i> | Effect | <i>P</i> | Effect | <i>P</i> |
| Ovenbird | NTM | + | 0.007 | | NS | | NS | - | 0.010 |
| Red-eyed Vireo | NTM | + | 0.001 | | NS | | 0.001 | + | 0.039 |
| Black-throated Green Warbler | NTM | + | 0.098 | - | 0.092 | + | 0.072 | | NS |
| Mourning Warbler | NTM | + | 0.064 | | NS | | NS | | NS |
| Tennessee Warbler | NTM | | NS | - | <0.001 | | NS | - | 0.023 |
| Yellow Warbler | NTM | | NS | | NS | | NS | - | 0.023 |
| Chipping Sparrow | NTM | | NS | - | 0.021 | | NS | | NS |
| Swainson's Thrush | NTM | | NS | | NS | | NS | - | 0.061 |
| Western Tanager | NTM | + | (0.008) | | NS | | NS | | NS |
| Rose-breasted Grosbeak | NTM | | NS | - | (0.020) | - | 0.019 | - | <0.001 |
| Ruby-crowned Kinglet | NTM | | NS | - | 0.071 | | NS | - | 0.088 |
| Magnolia Warbler | NTM | | NS | | NS | + | 0.056 | | NS |
| Western Wood Peewee | NTM | | NS | - | (0.009) | | NS | + | 0.038 |
| White-throated Sparrow | SD | + | 0.053 | | NS | | NS | | NS |
| Yellow-rumped Warbler | SD | + | 0.015 | | NS | - | (0.008) | | NS |
| Winter Wren | SD | + | (0.058) | | NS | | NS | | NS |
| Brown-headed Cowbird | SD | + | 0.012 | | NS | | NS | | NS |
| Hermit Thrush | SD | | NS | + | 0.090 | | | | |
| House Wren | SD | + | (0.012) | + | (0.087) | | NS | | NS |
| Red-breasted Nuthatch | RES | | NS | - | (0.004) | - | 0.022 | | NS |
| Black-capped Chickadee | RES | | NS | - | 0.088 | | NS | | NS |

[†] Neotropical migrants (NTM), permanent residents (RES), and short-distance migrants (SD) (after Godfrey 1986, Anonymous 1991).

[‡] Change in mean abundance relative to that observed in the controls.

[§] All *P* values are based on *t* tests, except those in parentheses, which are from Mann-Whitney tests; NS, nonsignificant.

munity through local extinctions and recolonizations, but no decrease in species richness after fragmentation. Contrary to our prediction of steeper slopes and lower intercepts, we detected no significant change in the species-area relationships either within, or between, treatment and control sites in response to experimental fragmentation. The only significant change in species richness in any size class occurred in the 1-ha connected fragments, where the mean in 1995 (two years postfragmentation) was 10.0 species, a substantial increase from 4.7 species in 1994 (one year postfragmentation) and 6.0 species in 1993 (prefragmentation), and significantly higher than the mean of 4.3 species in 1-ha isolated fragments, and 5.0 species in 1-ha controls, in the same year. However, numbers of probable breeders remained constant at roughly three species in each year. We propose that the proximity of the sampling stations in the 1-ha connected fragments to the adjacent, 100 m wide riparian buffer strip increased the probability that species moving through or breeding in those buffers were incidentally sampled, relative to either the 10-ha or 40-ha connected fragments, or any of the isolated fragments.

Community collapse or relaxation following habitat fragmentation (Brown 1971), as reflected by changes in species-area relationships, is usually measured over the course of decades or longer, and most cases of species loss from forest fragments are from areas where regional deforestation occurred long ago. This exper-

imental study, although more rigorous than retrospective approaches, is short-term. However, we might expect major responses to our manipulation to occur now rather than later, as regrowth in the cut blocks surrounding the fragments is rapid (>1.5 m in two years), potentially ameliorating negative effects (see also Stouffer and Bierregaard 1995). In designing this experiment, we estimated that we would be able to detect a 20% loss of species from a 50-ha area (Schmiegelow and Hannon 1993), which should exceed the level of variation naturally present in the system. Mean annual variation in species number in a 50-ha control area over the 3-yr course of this study (extrapolated from Table 3) was 10.9%, reflecting an estimated loss of three species from 1993–1994, and a recovery of these three species from 1994–1995. Therefore, an effect size of 20%, roughly twice the variability inherent in the system, should have been readily detected, particularly since the estimates of variance we used for our original power analyses are higher than those we observed.

We attempted to further refine our ability to detect meaningful changes in species richness by defining a subset of species that we classed as probable breeders. However, this approach was limited by our reliance on point count data and by problems associated with sampling rare species. Although these limitations were consistent across treatments and years and, thus, did not bias our results, some species may not have been sampled adequately, due either to breeding phenology or

to detectability, given our criteria for defining probable breeders (see Table 1).

Patterns in species diversity and turnover

Changes in diversity.—The absence of a relationship between bird diversity and area in both treatments and controls before fragmentation is not surprising, given our experimental design and the use of the log series α index. We attempted to minimize habitat variation through careful selection of our study areas, and the α index removes the effect of sample size, so the two factors that influence species–area relationships were standardized. Hence, the occurrence of a significant diversity–area relationship (and true species–area relationship) in the isolated fragments following fragmentation, but not in other sites, is particularly interesting. The relationship resulted primarily from a reduction in diversity in the 1-ha and 10-ha isolates, but there was no consistent pattern with respect to either changes in numbers of individuals or changes in numbers of species across years or among replicates. Habitat fragmentation created diversity relationships in the isolated fragments consistent with predictions from island biogeography theory, and it is likely that changes in both population sizes and habitat diversity were important factors. Whether these will lead to longer term species loss is not known.

Changes in species composition.—The significant positive relationship that we observed between community similarity over time and area is consistent with results from other studies (e.g., Hinsley et al. 1995), and suggests that community stability increases with size. Over the course of this study, the communities in isolated fragments experienced slightly, but significantly, higher species turnover than in either connected fragments or control sites, with the effect being most pronounced in smaller isolates, consistent with our second prediction. Since there was no significant loss of species from these areas over the same time period (1993–1995), there was substantial replacement of species present in the prefragmentation community. The resident species we studied, all of which prefer older forest (Schieck and Nietfeld 1995), most frequently disappeared from fragmented areas. However, the pattern of replacement by other species was not consistent, supporting the notion of community instability that was also suggested by changes in diversity.

Changes in abundance

Several studies have documented crowding of birds in habitat fragments immediately postfragmentation, followed by relaxation of the community in subsequent years (Whitcomb et al. 1981, Bierregaard and Lovejoy 1989, Darveau et al. 1995). We found no absolute increase in overall abundance of birds in the isolated fragments immediately postfragmentation. However, although bird abundance decreased in the controls in 1994, there was a significant increase in the isolated

fragments relative to the controls, suggesting a “crowding” effect. We detected no differences in the overall abundance of birds between treatments and controls two years after fragmentation, consistent with our third prediction that increases in abundance would be temporary.

When we examined the structure of the communities more closely, we discovered that abundance responses varied with respect to migratory strategy of the birds. Overall, Neotropical migrants exhibited the strongest crowding effect immediately after fragmentation, short-distance migrants exhibited an intermediate level of crowding, and numbers of residents remained comparable among treatments and controls. These differences may be related, in part, to breeding phenology. Harvesting was completed in February; therefore, resident birds had a longer time to respond to the experimental fragmentation by prospecting for new territories prior to breeding. However, the overall low densities of resident species might also have made crowding difficult to detect. Returning migrants were more constrained in their ability to respond to the habitat alteration, Neotropical migrants most so, given the narrow window of time in which territory establishment, nest-building, laying, incubation, and rearing must take place. This effect would decline over time, because adult mortality would reduce philopatry in subsequent seasons, and juveniles might prospect for future territories at the end of the breeding season, prior to migration (Brewer and Harrison 1975, Adams and Brewer 1981, Morton et al. 1991). Hagan et al. (1996), based on results from Bierregaard et al. (1992) for resident birds in tropical forests, predicted that it could take two or three breeding seasons (years) for elevated Neotropical migrant numbers to return to prefragmentation levels, or for negative numerical effects to develop, in temperate regions.

Two years following fragmentation, Neotropical migrants and residents were less abundant in both the isolated and connected fragments than in the controls, but there was no difference among short-distance migrants. This pattern also held at the species level: all 10 bird species that exhibited significant negative responses to fragmentation in the isolated or connected sites were either Neotropical migrants or residents, a nonrandom result with respect to community composition. Species preferring older forest accounted for seven of the 10 species that declined in either the isolated or connected fragments, whereas the four species that increased in abundance following fragmentation either prefer younger forest or are not typically forest species (see Semenchuck 1992, Schieck and Nietfeld 1995). Several additional species, also Neotropical migrant, old-forest specialists, showed nonsignificant downward trends in abundance.

These results are generally consistent with studies from both eastern deciduous forests (Ambuel and Temple 1983, Lynch and Whigham 1984) and the eastern

boreal forest (Darveau et al. 1995), and with the widespread population declines in forest-breeding Neotropical migrants reported from more eastern regions of their breeding range (e.g., Robbins et al. 1989, Askins 1995). Ambuel and Temple (1983) suggested that some forest-dwelling, long-distance migrants were actually excluded from forest fragments by forest edge and farmland species (most of which were short-distance migrants or residents), through competition, predation, or nest parasitism. Darveau et al. (1995) report a decrease in forest-dwelling species, and an increase in ubiquitous species in riparian buffer strips created by clear-cutting of adjacent areas. From Table 1 of their study, we classified species in these groups by their migratory habit: 71.4% of all territories of forest-dwelling species belonged to Neotropical migrants, and 94.3% of the territories of ubiquitous species were held by short-distance migrants. In all cases, response of bird species to fragmentation differed with respect to migratory habit.

Connectivity and fragmentation effects

Our results indicate that the connected fragments were less affected by fragmentation than were the isolated areas, consistent with our fourth prediction, but overall differences were small. The larger effective sizes of the connected fragments may, alone, have been enough to lessen the effects seen in the smaller, isolated fragments, since the habitat in the adjacent buffer strips increased the relative area of the 1-ha and 10-ha connected sites by 100% and 40%, respectively. Also, the availability of adjacent habitat in the buffer strips, and the fact that the amount of habitat removed around the connected fragments (and, consequently, the potential pool of displaced individuals) was 25% lower than for the isolated fragments, would dilute any crowding effect. In addition, concurrent studies in the area indicated that forest birds moved through the adjoining buffer strips much more frequently than across clearcuts, and that juvenile dispersers used the buffer strips as corridors (Machtans et al. 1996), which should further mitigate any fragmentation effects.

These results also suggest that distances as small as 200 m can effectively isolate many forest birds during the breeding season (see also Soulé et al. 1988). Surveys of clearcuts adjacent to both the connected and isolated fragments recorded very few movements of birds associated with older forest across such areas (Machtans et al. 1996; F. K. A. Schmiegelow, *unpublished data*). Experimental work by A. Desrochers and S. J. Hannon (*in press*) supports the idea that clearcuts represent behavioral, rather than physiological, barriers to forest birds, and argues for the consideration of constraints beyond dispersal ability per se.

Natural and human-induced disturbances in boreal systems

The spatial and temporal patchiness that characterizes the boreal forest, and the natural disturbance re-

gimes that have created such mosaics, have led to suggestions that bird species occupying these habitats may be preadapted to large-scale disturbance and fragmentation (e.g., Welsh 1987). Support for this comes primarily from work in western Palaearctic forests (see Haila 1994), where the numerically dominant species tend to be habitat generalists (Haila et al. 1994, Hansson 1994). However, Neotropical migrants, most of which are habitat specialists, predominate in the Nearctic (Mönkkönen 1994, Mönkkönen and Welsh 1994). Such specialization might compromise their ability to adjust to the rapid landscape changes brought about by industrial forestry. Secondly, there is a long history of human-induced habitat change in western Palaearctic forests, leading Angelstam (1992) to suggest that many of the species sensitive to forest fragmentation became extinct hundreds of years ago, thus confounding conclusions based on contemporary patterns of response. The bird communities of the western Nearctic boreal forest have not been exposed to such human-induced landscape alterations, and might contain more sensitive species.

Nevertheless, some studies from Palaearctic boreal forests have identified groups of birds sensitive to fragmentation and loss of older forest (e.g., Helle and Järvinen 1986, Väisänen et al. 1986). In particular, woodpeckers and other hole-nesters (Angelstam and Mikusiński 1994, Virkkala et al. 1994) and several additional northern taiga species (Virkkala 1987) are of concern due to declining numbers. Many of these species have Nearctic counterparts in our resident birds (see Haila and Järvinen 1990). Furthermore, recent studies in both Palaearctic and Nearctic boreal forests indicate that small-scale gap dynamics may play an important role in structuring the forest at both local and regional scales (Kuuluvainen 1994; S. G. Cumming, F. K. A. Schmiegelow, and P. J. Burton, *unpublished manuscript*), arguing against the uncritical acceptance of a natural disturbance paradigm based on large, catastrophic events such as fire and insect outbreaks.

The role of the landscape matrix

Studies of fragmentation conducted in agricultural or suburban landscapes have often concluded that losses of species, or declines in abundance, are the result of increased rates of nest parasitism and predation by edge-related species (e.g., Brittingham and Temple 1983, Wilcove 1985, Martin 1992b). Fragmentation by agriculture favors cowbirds, since it provides both feeding and breeding habitats. Fragmentation by forest harvesting changes forest age, composition, and structure, but does not create feeding habitat for cowbirds. We detected no significant change in numbers of Brown-headed Cowbirds, an obligate nest parasite, two years after fragmentation, and brood parasitism rates in our study area are extremely low (M.-A. Villard and S. J. Hannon, *unpublished data*). We also doubt that predation will significantly lower nesting success, since

forest harvesting is not creating a matrix that similarly favors many nest predators. In an experiment in adjacent forest, Cotterill (1996) found no immediate increase in overall predation rates on artificial nests as a result of habitat fragmentation.

The influence of regional patterns of forest cover on the response of birds to fragmentation is being increasingly recognized (e.g., Askins and Philbrick 1987, Freemark and Collins 1992, McGarigal and McComb 1995, Robinson et al. 1995). When large tracts of forest exist regionally, populations of birds in smaller, more isolated patches of forest may be maintained through a "rescue effect" (Brown and Kodrick-Brown 1977). Presently, our study area exists in a landscape matrix dominated by older, mixed forest, which may buffer local impacts of fragmentation. The boreal mixed-wood mosaic will remain forest dominated, but the relative proportions of stands of different age and composition are likely to change dramatically as harvesting proceeds.

Cumming et al. (1994) modelled various boreal mixed-wood management strategies, concluding that, without substantial reductions in harvest levels or increases in operating costs, most of the region's older, mixed stands will be converted to younger, single-species stands. Habitat loss may result in overall population declines of certain bird species, but this is not a fragmentation effect per se (see Haila 1986). However, area-related edge effects, such as reduction in habitat quality due to changes in vegetation (Matlack 1993, Esseen 1994, Pettersson et al. 1995), and competitive exclusion or replacement by species able to utilize the surrounding matrix (e.g., Ambuel and Temple 1983, Haila et al. 1989, Ims and Rolstad 1993), are likely to exacerbate habitat loss and increase the minimum area required by old-forest specialists. Important considerations include the ability of individuals to successfully reproduce in remnant patches of older forest, the availability of such patches over time, and changes in potential edge effects over time as the surrounding forest regenerates. As Haila et al. (1993), among others, have pointed out, a simplified concept of fragmentation is not adequate when considering forest patches within dynamic habitat mosaics.

CONCLUSIONS

Although we observed some significant negative effects of the experimental fragmentation, consistent with our predictions, and some interesting trends, magnitudes were small, given the extent of our manipulations. Where effects did occur, they were most pronounced in the smaller isolates, and Neotropical migrant and resident species exhibited the greatest sensitivity. Responses were generally smaller or nonexistent in the connected fragments relative to the isolated fragments. It appears that the breeding boreal bird community is quite resilient to major disturbances. However, there are several important caveats to our conclusions. First,

we measured only short-term, broad-scale responses based on relatively coarse community measures. The nonsignificant trends we observed could become significant declines or losses over time. We are continuing to sample the fragments in order to monitor longer term effects. Furthermore, estimates of abundance may not provide a reliable indicator of habitat quality (Van Horne 1983). Ongoing studies of avian productivity address this concern (F. K. A. Schmiegelow, M.-A. Villard and S. J. Hannon). Second, we did not analyze data from several groups of bird species that might be more sensitive to fragmentation at this scale. For example, woodpeckers and raptors, many of which are resident species, generally require larger breeding and foraging areas than do the species reported here. We have expanded our surveys to better sample woodpeckers, and are currently documenting changes in raptor communities over a larger scale (B. Olsen, G. Court, and S. J. Hannon). Third, any effects may have been mitigated by the large areas of old, mixed forest still present regionally. The availability of such habitat in the future will be substantially reduced, due to the widespread industrial forestry in progress in the boreal mixed-wood forest.

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APPENDIX

Abundance of bird species in older, aspen-dominated forest, at Calling Lake, Alberta, Canada, from 1993 to 1995. Species are listed from most to least abundant.

| Common name | Scientific name | Status† | Abundance‡ | Detections§ |
|------------------------------|-----------------------------------|---------|------------|-------------|
| White-throated Sparrow | <i>Zonotrichia albicolis</i> | SD | 3715.5 | 3856 |
| Yellow-rumped Warbler | <i>Dendroica coronata</i> | SD | 2420.5 | 2452 |
| Ovenbird | <i>Seiurus aurocapillus</i> | NTM | 1962.0 | 1974 |
| Red-eyed Vireo | <i>Vireo olivaceus</i> | NTM | 1418.5 | 1427 |
| Least Flycatcher | <i>Empidonax minimus</i> | NTM | 1411.0 | 1441 |
| Black-throated Green Warbler | <i>Dendroica virens</i> | NTM | 1239.0 | 1241 |
| Mourning Warbler | <i>Oporornis philadelphia</i> | NTM | 1144.5 | 1146 |
| Tennessee Warbler | <i>Vermivora peregrina</i> | NTM | 710.5 | 708 |
| American Redstart | <i>Setophaga ruticilla</i> | NTM | 706.0 | 710 |
| Connecticut Warbler | <i>Oporornis agilis</i> | NTM | 702.5 | 703 |
| Yellow Warbler | <i>Dendroica petechia</i> | NTM | 598.5 | 601 |
| Chipping Sparrow | <i>Spizella passerina</i> | NTM | 542.5 | 545 |
| Yellow-bellied Sapsucker | <i>Sphyrapicus varius</i> | SD | 488.0 | 618 |
| Swainson's Thrush | <i>Catharus ustulatus</i> | NTM | 450.0 | 500 |
| Western Tanager | <i>Piranga ludoviciana</i> | NTM | 431.0 | 460 |
| Rose-breasted Grosbeak | <i>Pheucticus ludoviciana</i> | NTM | 387.0 | 393 |
| Winter Wren | <i>Troglodytes troglodytes</i> | SD | 367.0 | 369 |
| Red-breasted Nuthatch | <i>Sitta canadensis</i> | RES | 298.5 | 308 |
| Warbling Vireo | <i>Vireo gilvus</i> | NTM | 228.0 | 229 |
| Solitary Vireo | <i>Vireo solitarius</i> | NTM | 211.5 | 212 |
| Brown Creeper | <i>Certhia americana</i> | RES | 196.5 | 208 |
| Black-capped Chickadee | <i>Parus atricapillus</i> | RES | 165.5 | 194 |
| Brown-headed Cowbird | <i>Molothrus ater</i> | SD | 160.0 | 186 |
| Lincoln's Sparrow | <i>Melospiza lincolni</i> | NTM | 106.5 | 107 |
| American Robin | <i>Turdus migratorius</i> | SD | 105.5 | 119 |
| Ruby-crowned Kinglet | <i>Regulus calendula</i> | SD | 105.0 | 105 |
| Philadelphia Vireo | <i>Vireo philadelphicus</i> | NTM | 98.0 | 98 |
| Dark-eyed Junco | <i>Junco hyemalis</i> | SD | 96.5 | 98 |
| Pine Siskin | <i>Carduelis pinus</i> | SD | 82.5 | 91 |
| Hermit Thrush | <i>Catharus guttatus</i> | SD | 78.5 | 84 |
| Magnolia Warbler | <i>Dendroica magnolia</i> | NTM | 60.0 | 60 |
| Cedar Waxwing | <i>Bombycilla cedrorum</i> | SD | 55.5 | 65 |
| White-winged Crossbill | <i>Loxia leucoptera</i> | SD | 53.0 | 56 |
| Western Wood Peewee | <i>Contopus sordidulus</i> | NTM | 46.5 | 47 |
| Black and White Warbler | <i>Mniotilta varia</i> | NTM | 44.5 | 46 |
| Golden-crowned Kinglet | <i>Regulus satrapa</i> | SD | 42.5 | 48 |
| House Wren | <i>Troglodytes aedon</i> | SD | 37.0 | 37 |
| Blackpoll Warbler | <i>Dendroica striata</i> | NTM | 26.5 | 27 |
| Purple Finch | <i>Carpodacus purpureus</i> | SD | 18.5 | 19 |
| Boreal Chickadee | <i>Parus hudsonicus</i> | RES | 16.0 | 22 |
| Orange-crowned Warbler | <i>Vermivora celeta</i> | NTM | 14.0 | 14 |
| Canada Warbler | <i>Wilsonia canadensis</i> | NTM | 13.5 | 14 |
| Common Yellowthroat | <i>Geothlypis trichas</i> | NTM | 8.0 | 8 |
| Alder Flycatcher | <i>Empidonax alnorum</i> | NTM | 8.0 | 9 |
| Northern Oriole | <i>Icterus galbula</i> | NTM | 8.0 | 8 |
| Bay-breasted Warbler | <i>Dendroica castanea</i> | NTM | 6.0 | 6 |
| White-breasted Nuthatch | <i>Sitta carolinensis</i> | RES | 6.0 | 6 |
| Eastern Phoebe | <i>Sayornis phoebe</i> | SD | 5.0 | 5 |
| Olive-sided Flycatcher | <i>Contopus borealis</i> | NTM | 5.0 | 5 |
| Evening Grosbeak | <i>Coccothraustes vespertenus</i> | SD | 3.5 | 4 |
| Palm Warbler | <i>Dendroica palmarum</i> | NTM | 3.0 | 3 |
| Song Sparrow | <i>Melospiza melodia</i> | SD | 3.0 | 3 |
| Clay-colored Sparrow | <i>Spizella pallida</i> | SD | 2.0 | 2 |
| Cape May Warbler | <i>Dendroica tigrina</i> | NTM | 2.0 | 2 |
| Common Redpoll | <i>Carduelis flammea</i> | SD | 2.0 | 2 |
| Blackburnian Warbler | <i>Dendroica fusca</i> | NTM | 1.0 | 2 |
| Yellow-bellied Flycatcher | <i>Empidonax flaviventris</i> | NTM | 1.0 | 1 |
| American Goldfinch | <i>Carduelis tristis</i> | SD | 0.5 | 1 |
| Savannah Sparrow | <i>Passerculus sandwichensis</i> | SD | 0.5 | 1 |

† Residency status indicated for Neotropical migrants (NTM), short-distance migrants (SD), and residents (RES) (after Godfrey 1986, Anonymous 1991).

‡ Weighted abundance over 3-yr study period (1993–1995) (see *Methods* for explanation).

§ Total number of detections over 3-yr study period (1993–1995).