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Cover: Male (left) and female Scarlet-banded Barbet, a new species from the cloud forest in eastern Peru. See O'Neill et al., pages 569–577. From a watercolor painting by Daniel F. Lane.

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SHORT-TERM EFFECTS OF TIMBER HARVEST ON ABUNDANCE, TERRITORY CHARACTERISTICS, AND PAIRING SUCCESS OF OVENBIRDS IN RIPARIAN BUFFER STRIPS

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ABSTRACT.—In managed forests, riparian buffer strips typically are maintained to protect water quality. If properly designed, buffer strips also may act as wildlife reserves. However, forest managers have lacked the information to develop standards for buffer strips to maximize benefits for wildlife species. We assessed the conservation potential of 20-, 100-, and 200-m wide buffers for an area-sensitive songbird in boreal mixed-wood forest in Alberta. We measured abundance, territory characteristics, and pairing success of Ovenbirds (*Seiurus aurocapillus*) at treatment and control lakes one year before and after upland timber harvest. After harvest, Ovenbirds were absent from 20-m buffer strips. Harvesting did not significantly influence abundance or territory size in 100-m or 200-m buffers, although territories generally became narrower. Postharvest territory position did not change in 200-m buffers, but territories in 100-m strips shifted lakeward and included more habitat adjacent to the riparian edge than before harvest. Despite this shift in territory position, males that occupied 100-m strips successfully attracted mates. High availability of regional forest cover may have muted the more pronounced effects of habitat alteration observed in other studies. Our research is among the first to evaluate individual behavioral responses to the creation of forest edges. Our data indicate that 20-m buffer strips do not support breeding Ovenbirds, whereas 100- and 200-m buffers retain Ovenbirds during the year following harvest. Long-term harvest effects may differ from those we monitored and require study, particularly as timber extraction increases in the boreal mixed-wood ecoregion. *Received 5 October 1998, accepted 7 December 1999.*

FORESTS THAT BORDER wetlands, streams, and lakes generally are characterized by an abundance and high diversity of wildlife (Budd et al. 1987, Gregory et al. 1991). In industrial timberlands, forest managers protect these riparian forests in buffer strips that are designed to safeguard water quality (Martin and Pierce 1980, Hornbeck et al. 1986). Although little information exists to assess their habitat value (Johnson and Brown 1990, Darveau et al. 1995), buffers also could act as wildlife reserves. However, research indicates that cutting upland forest can result in the replacement of forest-interior songbirds with edge-adapted species (Triquet et al. 1990, Johnson and Brown 1990, Darveau et al. 1995, Machtans 1996). Unfortunately, low replication and inconsistency among previous studies preclude the development of sound standards for buffer widths. Consequently, forest managers require more information to guide songbird conservation efforts in riparian forests.

Increasing timber activity in the boreal mixed-wood forest of north-central Alberta provided an opportunity to examine the influence of buffer-strip width on area-sensitive bird species. In this ecoregion, more than 80,000 km^2 of woodland has been leased to pulp and paper companies in recent years (Alberta Environmental Protection 1996). Management plans call for checkerboard clearcutting of stands dominated by trembling aspen (*Populus tremuloides*) in a two- to three-pass harvesting system. A minimum of 10 years will separate passes, and rotation lengths are projected to be 60 to 70 years. Managers will maintain 100-m-wide buffer strips of riparian forest adjacent to lakes larger than 4 ha (Alberta-Pacific 1993). In many areas, after the second and third harvesting passes, forests older than 60 to 70 years will be concentrated in these zones. Consequently, buffers may play an important role in the long-term conservation of the re-

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gion's native songbirds that rely on older forests.

The Ovenbird (*Seiurus aurocapillus*) is a Neotropical migratory warbler and a common breeder in mature (>30 years old) aspen-dominated stands of Alberta's boreal mixed-wood forest (Westworth and Telfer 1993, Schieck and Nietfeld 1995). In riparian buffer strips, Ovenbird density is width-sensitive, decreasing as buffers narrow (Stauffer and Best 1980, Triquet et al. 1990, Machtans 1996, Whitaker and Montevecchi 1999). However, density alone is an insufficient index of habitat quality (Van Horne 1983, Vickery et al. 1992). Hagan et al. (1996) argued that habitat-suitability assessments should use pairing and behavioral data to complement density estimates. Over the past decade, several studies have examined rates of Ovenbird pairing success to evaluate quality of forest tracts in both agricultural (Gibbs and Faaborg 1990, Porneluzi et al. 1993, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998) and silvicultural landscapes (King et al. 1996, Sabine et al. 1996). However, to our knowledge, no study has investigated effects of timber management on songbird behavior. Behavioral information, especially that concerning territory characteristics, may be particularly valuable in determining the conservation potential of riparian buffer strips. Compression, distortion, or adjustments in territory position could reduce the fitness of territory-holders in a variety of ways, including depletion of food, increased costs of territory maintenance, heightened interspecific competition, and mating failure. Therefore, the size, shape, and position of Ovenbird territories in riparian forests warrant measurement before and after upland timber harvest.

We assessed the value of buffer strips to Ovenbirds in a pre- and postharvest study with contemporary controls. We evaluated abundance data, detailed territory maps, and pairing success of males to measure the short-term response of Ovenbirds to upland timber harvest in buffers strips of 20, 100, and 200 m in width. We hypothesized that suitability of buffer strips would increase with width, such that 20-m buffers would be the least suitable and 200-m buffers would provide the most suitable habitat, relative to controls. Specifically, we predicted that (1) Ovenbirds would be absent from 20-m buffer strips; (2) their numbers would be reduced, their territories would be configured differently than before harvest, and males would have reduced pairing success in 100-m buffers; and (3) effects of harvest on abundance, territory characteristics, and pairing success would be least evident in 200-m buffers.

METHODS

Study areas and experimental design.—We conducted the research in the boreal mixed-wood forest of north-central Alberta, a low-relief mosaic of trembling aspen, balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*) stands. Although forest cover dominates this ecoregion, shallow lakes, wetlands, roads, cutblocks, and seismic lines are also characteristic features. All study sites were located in 50- to 100-year-old forests, where aspen and balsam poplar comprised 60 to 100% of the canopy. To varying degrees, white spruce, white birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) were present in the subcanopy or as minor canopy components. Shrub species were heterogeneous in dispersion and structure, consisting primarily of prickly rose (*Rosa acicularis*), lowbush cranberry (*Viburnum edule*), wild raspberry (*Rubus idaeus*), and Saskatoon berry (*Amelanchier alnifolia*). Herb, fern, and moss species made up the ground vegetation, which typically ranged from 10 to 30% in cover.

Study sites were distributed among three research areas: Lac La Biche, South Calling Lake, and South Pelican Hills (Fig. 1). Each area contained three treatment lakes, with buffer-strip widths of 20 m, 100 m, and 200 m. A fourth lake, isolated from clearcuts by at least 800 m, served as a control at each area. This experimental design was developed by the Terrestrial and Riparian Organisms, Lakes, and Streams (TROLS) project at the University of Alberta, a multidiscliplinary investigation into effects of buffer width on terrestrial and aquatic ecosystems. During the winter of 1996–1997, after the first field season, 3.6 to 39.5% ($\bar{x}$ = 18.5%) of the forest area within 800 m of treatment lakes was harvested in blocks of 11 to 38 ha. The treatment created two forested buffers of the prescribed width at each lake. Unharvested blocks occurred adjacent to the remainder of riparian forest surrounding the lakes. Cutblocks retained approximately 0 to 5% of standing timber in small, scattered clumps. Combined, the three research areas contained six replicates of 100-m and 200-m treatments. Owing to a harvesting error at one 20-m site, we sampled five replicates of this width class. Four study sites were located on each undisturbed lake, giving a total of 12 control replicates.

Estimating abundance.—During the breeding seasons before (1996) and after (1997) harvest, we per-

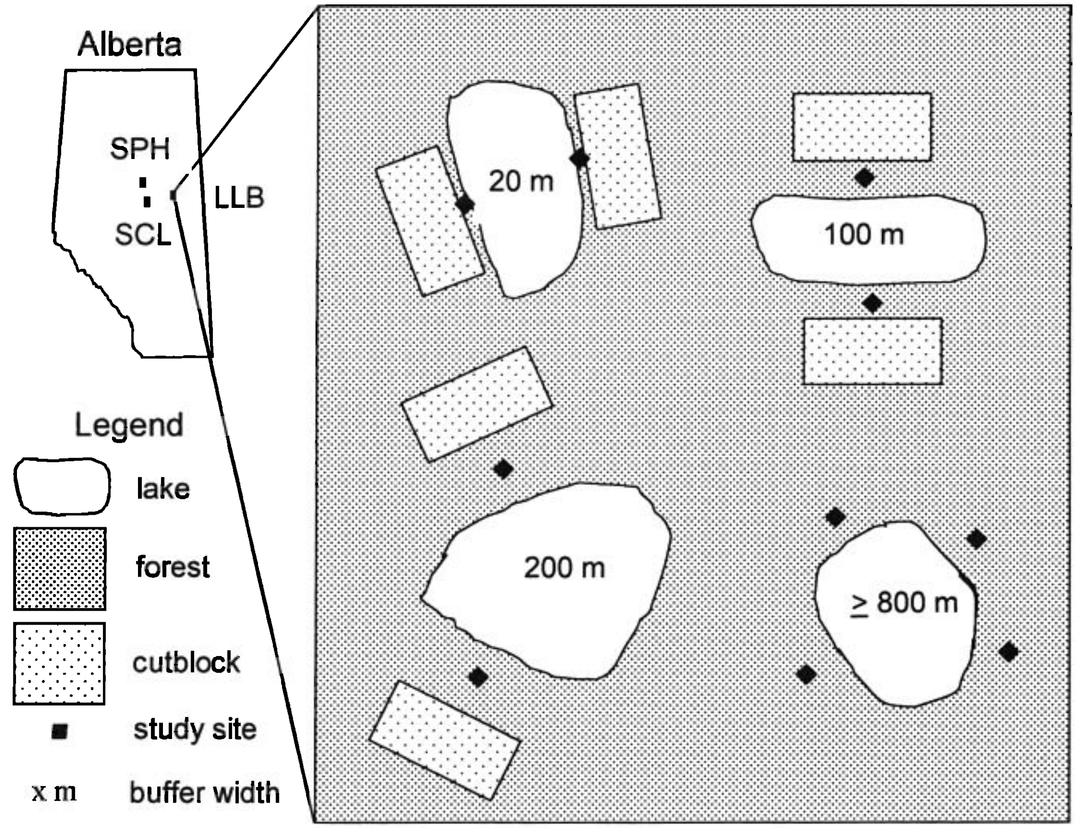

FIG. 1. Schematic diagram of experimental design including location of research areas in Alberta, Canada. LLB = Lac La Biche, SPH = South Pelican Hills, and SCL = South Calling Lake.

formed extensive spot mapping to estimate Ovenbird abundance at all sites. We surveyed sites in 400-m-long grids following the treeline along the shore and extending back into the forest; each grid was composed of 50 × 50 m cells (Fig. 2). Grids extended 100 m upland at 20-m and 100-m lakes and 200 m upland at 200-m and control lakes. Modifications of the rectangular grid design, required at sites with nonlinear lakeshores, resulted in slight variations among sites in grid shape and size. We assigned a zone number to each row of grid cells, with zone 1 situated adjacent to the lake. A transect bisected each zone lengthwise, with spot-mapping stations located at 50-m intervals (Fig. 2). The lower half of each control site (zones 1 and 2) was designated as a reference for 100-m buffer strips. The entire control site (zones 1 to 4) served as a reference for 200-m buffers.

Between 20 May and 4 July in 1996 and 1997, each of several trained technicians sampled two grids per morning. We alternated observers, entry points, and sampling sequences to minimize bias and visited each grid six times at intervals of five to seven days. We spot-mapped the full songbird assemblage at a rate of 30 min per transect between sunrise and 1000 MST. Spot maps included birds heard singing up to 50 m off the surveyed grid.

We also conducted postharvest surveys for Ovenbirds in three buffers that ranged in width from 40 to 80 m. At weekly intervals, beginning the fourth week of May, observers spent one hour between sunrise and 1000 searching each strip for Ovenbirds. Surveys were terminated at all of these buffers after four visits because no Ovenbirds were detected.

We compiled maps on transparent sheets and distinguished territories according to patterns of song-perch clusters and counter-singing events. A territory was counted as on the grid if most of the song perches occurred within the grid's boundaries. If a given male's on-grid and off-grid song perches were equal in number, we drew a polygon around the points. If most of a polygon's area overlapped the grid, the territory was considered to be on the grid. If a minor portion of the polygon overlapped the grid, it was not counted. Rather than assign fractional values to territories, we assumed that the sum of partial territories excluded from counts equaled the sum of partial territories added. We confirmed the accuracy of this approach with detailed territory

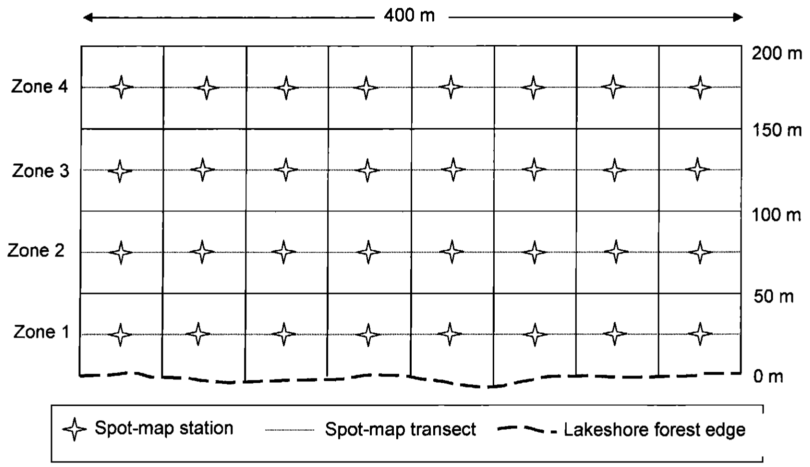

FIG. 2. A sampling grid with spot-mapping stations, transects, and zones designated according to proximity to lakeshore forest edge.

maps, described below. Finally, we corrected abundance estimates to account for differences in grid size that arose from the variability of lakeshore contours.

Territory mapping.—To measure territory characteristics we performed intensive territory mapping at a subset of grids in South Calling Lake and Lac La Biche only. In 1996, we mapped territories on 13 grids, four at 100- and 200-m buffers and five at controls. In 1997, we added a control site and three 100-m buffer strips to the territory-mapping protocol. The added buffer strips abutted 1- to 2-year-old clearcuts at three different lakes. Because Ovenbirds were not expected to occur in 20-m strips after harvest, we did not map territories in this width class.

Each year between 20 May and 12 July, we visited grids six to eight times at an average interval of seven days (range 5 to 10). We began observations 30 min before dawn by surveying 20 to 30 min for Ovenbirds. While walking a central transect through a strip's interior, we noted the approximate position of all males singing on the grid or from adjacent areas. In this manner, we determined where to concentrate our attention during the midmorning hours when activity was low. We then targeted individual males and mapped their activity, in sequence, for up to an hour. Late in the season, as activity subsided, the maximum observation period was abbreviated to 30 min. If a focal male went undetected for 15 min, we turned our attention to a neighboring territory and returned when time allowed. We alternated the sequence of focal observations with each visit so that time of day would not bias results. We ceased observations at either 1000 or after an hour without detections.

During late morning and early afternoon, we used an Ovenbird decoy and tape-recorded songs to lure territorial males into mist nets. We noted recaptures and banded newly captured birds with unique combinations of three plastic color bands and a Canadian Wildlife Service aluminum band. Color bands on one-third of the males (34 of 102) helped us distinguish among neighbors.

At season's end, we analyzed maps of movements, interactions, song perches, and simultaneous singing episodes to delineate each territory. We digitized each individual's song perches in the Geographical Resources Analysis Support System (GRASS), a geographic information system. To identify the minimum number of song perches necessary to delineate a territory, we first analyzed a subset of 13 territories that had more than 85 mapped song perches. We drew minimum convex polygons (MCPs) around randomly subsampled clusters of song perches, graphed polygon area versus number of song perches, and observed an asymptote at the 50-perch threshold (Lambert 1998). Therefore, we concluded that MCPs drawn around 50 song perches, mapped during five or more visits, adequately described Ovenbird territories. For the 13 thoroughly mapped birds, MCPs based on 50 perches constituted, on average, 0.87 ± SE of 0.03 and 0.85 ± 0.03 of the total areas used by those birds in 1996 and 1997, respectively.

Next, we drew MCPs around 50 randomly subsampled song perches for all territories that had at least 50 perches mapped ($n = 31$ in 1996, $n = 42$ in 1997). For each territory, GRASS calculated area (ha) and a circularity index $[(0.282 \times \text{perimeter})/(\text{area})^{1/2}]$ that varied between 1.0 for a circle and infinity for an infinitely long and narrow shape. An index of 1.12 represents a square. With GRASS, we also measured the length of each polygon's minor and major axis. We measured territory position by the minimum distance between a territory's boundary and the riparian forest edge, and also by the proportion of the territory area occurring in the 50-m zones.

Pairing success.—We performed focal observations of males to determine pairing success using methods modified from previous research. While mapping territories, we tracked individual males for up to 90 min over the course of the season (20 May to 12 July). Track time accumulated when the focal individual was in sight or in continuous song within 30 m of the observer. During this time, males that tolerated a nonvocal conspecific within 10 m were considered paired. Males were also considered to be paired when we heard a female's high *tsip* vocalization in the presence of a singing male (Sabine et al. 1996). This distinctive courtship call (Lein 1980) indicates the female's association with the male (Van Horn and Donovan 1994). Males that were not observed with a female after 90 min were considered unpaired, and those tracked for less than 90 min were classified as unknown.

We applied three precautions to increase the accuracy of our determination of pairing status. First, we tracked males for no more than 30 min during the first round of observations (20 May to 27 May), when some females may not have selected mates. Second, during succeeding rounds, we tracked males for a maximum of 60 min, no more than 30 min continuously. Finally, males had to have been tracked for at least 60 min before the incubation period, because pairs rarely are seen together during incubation. In two seasons, 67 of 78 known pairs (86%) were identified in 45 min of tracking time, and 76 (97%) were observed within 75 min. These figures validate 90 min as a reliable threshold for the determination of pairing status.

Data analysis.—We used t-tests, Wilcoxon signed-rank tests, and Mann-Whitney U-tests to compare abundance and territory variables between treatment and control groups and between years. The site (grid) served as the sample unit for tests, with territory characteristics described as the mean value among each site's territories. The number of territories with 50 or more song perches mapped in a given site and year ranged from one to six. The use of a site-based mean in statistical analyses was necessary to avoid pseudoreplication, because territory holders on each site were related either by direct interaction or by common association with site-specific habitat characteristics. Previous researchers (Porneluzi et al. 1993, Villard et al. 1993, Donovan et al. 1995, Hagan et al. 1996, King et al. 1996, Sabine et al. 1996) have made the questionable assumption of independence among male Ovenbirds that share the same forest tract.

We performed a post-hoc power analysis on each conventional test with GPOWER (Faul and Erdfelder 1992). In many comparisons, statistical power was low owing to small effect and sample sizes. We report results of conventional tests when power was moderate to high ($d \geq 0.65$, $\alpha = 0.1$), when power was sufficient to detect a significant effect ($P < 0.1$), and when the effect size was below the level considered to be small ($d < 0.2$, $\alpha = 0.1$; Cohen 1988). We selected a conservative α level to avoid Type II errors, because erroneous conclusions of no treatment effect might misguide management efforts.

When tests did not meet power requirements, we employed randomization testing based on a resampling approach that optimizes analyses of small data sets. We handled variables with one value per site (e.g. abundance) with the program RT 2.0 (Manly 1996). This program calculates the observed mean difference (OMD) between two samples, randomly reassigns data points to the two categories 1,000 times, and then generates a distribution of randomized mean differences (RMDs). If fewer than 10% of the absolute RMDs equal or exceed the OMD, the result is considered significant ($P < 0.1$). We compared abundance data, pre- versus postharvest, and treatment versus control categories in this manner. We also used RT 2.0 to compare the mean proportion of song perches occurring in a given zone between riparian and clearcut sites.

We handled blocked data, where multiple dependent values were reported for each site (e.g. territory size), with Randcomp 0.1 (Brzustowski 1997). This program calculates a grand mean from the site means in a given category and defines the OMD as the difference between grand means. It then randomly reassigns values to blocks and generates a distribution of randomized (grand) mean differences. As with RT 2.0, the proportion of absolute RMDs > OMD represents the index of significance (P).

Owing to lack of independence among neighboring males, the use of contingency tables in an analysis of pairing success was not possible without committing pseudoreplication. Furthermore, the small number of individuals on each site resulted in crude, site-specific proportional measures. Therefore, we dismissed the option of mean comparisons and chose to report overall proportions of paired males.

In the text and tables that follow, results from randomization tests are those that have P-values unaccompanied by test statistics. All results derived from conventional methods, except for those appearing in graphs, report test statistics with P-values.

RESULTS

Ovenbird abundance in buffer strips.—None of the five 20-m buffer strips contained Ovenbirds in 1997, the breeding season after harvest. Because we rarely observed Ovenbirds within 20 m of lakes in intact riparian forests (see below), this result is not surprising. Ovenbirds were also absent from three buffer strips, surveyed

TABLE 1. Abundance (number of territories per site) of Ovenbirds before and after harvest in 100-m and 200-m buffer strips and in undisturbed control sites in Alberta. Values are $\bar{x}$ ± SE.

Site class	n[a]	Before harvest	After harvest	Test statistic[b]	P
100-m buffer	6	1.40 ± 0.51	1.60 ± 0.24	$Z = -0.447$	0.66
100-m control	12	1.00 ± 0.21	0.50 ± 0.19	—	0.11
200-m buffer	6	2.50 ± 0.43	2.50 ± 0.43	$Z = 0.000$	1.00
200-m control	12	2.33 ± 0.38	2.25 ± 0.28	—	0.87

[a] Number of sites.

[b] Wilcoxon signed-rank test (Z-scores) and randomization test (no test statistic).

in 1997 only, that ranged in width from 40 to 80 m. Extensive spot mapping revealed no immediate postharvest effect on the abundance of Ovenbirds in 100-m or 200-m buffer strips (Table 1). Ovenbird numbers in undisturbed controls also remained stable between years.

Randomization analysis of 1997 territory-map data showed no difference in abundance between seven 100-m buffers ($\bar{x}$ = 1.31 ± 0.45) and six 100-m controls ($\bar{x}$ = 1.04 ± 0.35; P = 0.67). Likewise, Ovenbird numbers in four 200-m buffers ($\bar{x}$ = 3.31 ± 0.34) did not differ significantly from six 200-m controls ($\bar{x}$ = 3.04 ± 0.51; P = 0.67).

Territory dimensions.—Mean territory size decreased in 100- and 200-m buffers after harvest and increased in their respective controls. However, no changes were statistically significant (Table 2). In general, territory shapes ranged widely from compact to elongate before and after harvest. The index of circularity registered no significant difference between years in any treatment class. Nonetheless, there was evidence of territory compression in buffer strips. Both in 100-m and 200-m buffers, the mean length of minor territory axes decreased by about 30 m, compared with a decrease of less than 5 m in their respective control groups. This response was significant in 200-m buffers but not in 100-m buffers. Lengths of major axes were highly variable in all treatment classes, but no differences were significant (Table 2).

Territory position.—Harvest of upland timber caused a shift toward the lake in Ovenbird ter-

TABLE 2. Effect of upland harvest on territory size and shape of Ovenbirds. Values are $\bar{x}$ ± SE.

Site class	n[a]	Before harvest	After harvest	Test statistic[b]	P
		Territory size (ha)			
100-m buffer	4	1.76 ± 0.29	1.45 ± 0.33	—	0.53
100-m control	5	1.36 ± 0.10	1.68 ± 0.33	$Z = -0.944$	0.35
200-m buffer	4	1.60 ± 0.26	1.36 ± 0.06	—	0.50
200-m control	5	1.34 ± 0.11	1.65 ± 0.32	—	0.57
		Circularity[c]			
100-m buffer	4	1.42 ± 0.09	1.46 ± 0.10	—	0.80
100-m control	5	1.43 ± 0.03	1.51 ± 0.08	—	0.67
200-m buffer	4	1.43 ± 0.05	1.37 ± 0.03	—	0.48
200-m control	5	1.41 ± 0.03	1.53 ± 0.08	$Z = -0.944$	0.35
		Length of minor axis (m)			
100-m buffer	4	108.25 ± 15.22	76.67 ± 12.20	—	0.24
100-m control	5	111.00 ± 8.80	106.60 ± 5.78	—	0.72
200-m buffer	4	125.25 ± 11.40	97.25 ± 6.80	$Z = -1.826$	0.07
200-m control	5	108.00 ± 8.27	106.40 ± 4.97	—	0.89
		Length of major axis (m)			
100-m buffer	4	229.00 ± 19.94	251.00 ± 41.51	—	0.64
100-m control	5	177.40 ± 7.47	241.40 ± 55.59	—	0.37
200-m buffer	4	188.25 ± 21.15	192.50 ± 10.31	$Z = -0.365$	0.72
200-m control	5	179.00 ± 6.46	240.60 ± 55.73	—	0.37

[a] Number of sites.

[b] Wilcoxon signed-rank test (Z-scores) and Randcomp (no test statistic).

[c] Where 1.0 is a circle, 1.12 is a square, and infinity is an infinitely long and narrow shape. See Methods for calculation.

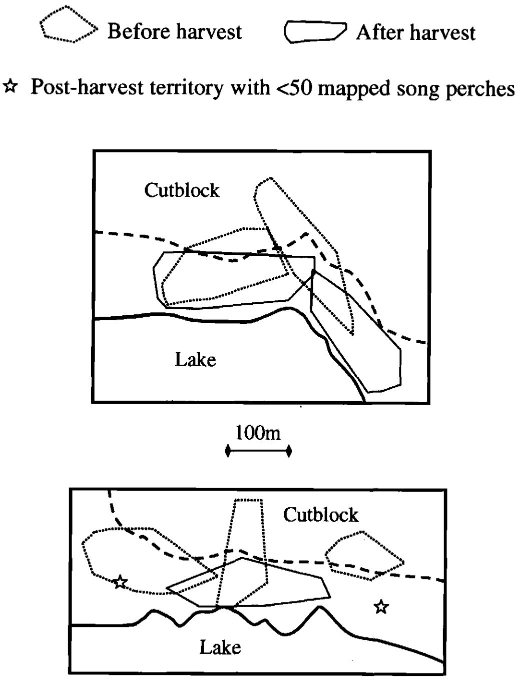

FIG. 3. Pre- and postharvest position of Ovenbird territories in two 100-m buffer strips.

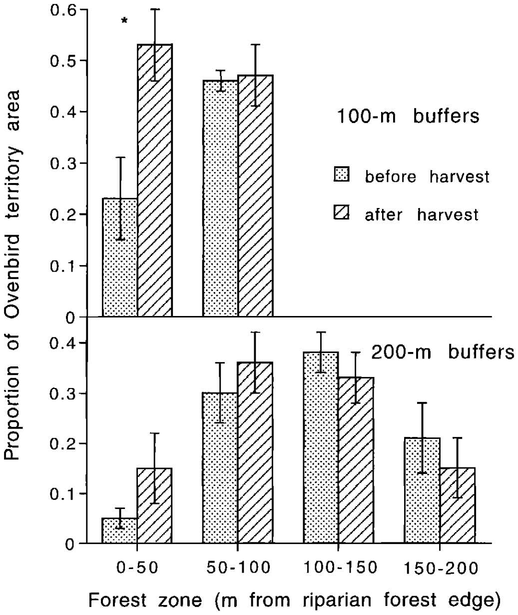

FIG. 4. Mean proportion of Ovenbird territory area (±SE) in designated zones within 100-m ($n = 4$ before harvest, $n = 3$ after harvest) and 200-m buffer strips ($n = 4$). Asterisk denotes $P = 0.05$ (one-tailed Wilcoxon signed-rank test).

ritory position within 100-m buffer strips (Fig. 3). The mean minimum distance from territory boundary to riparian forest edge decreased significantly from 16.54 ± 5.99 m ($n = 4$) before harvest to 6.33 ± 5.36 m ($n = 4$) after harvest ($Z = -1.60$, $P = 0.05$). A comparison of six 100-m buffers and six control sites in 1997 showed a more dramatic contrast. In unharvested areas, territories were positioned, on average, 48.25 ± 5.33 m from the riparian edge, whereas the mean distance in 100-m buffers was only 12.08 ± 5.94 m ($U = 0.00$, $P = 0.001$). At five 100-m control sites, territory proximity to the forest edge did not differ between 1996 ($\bar{x} = 31.53 \pm 4.73$ m) and 1997 ($\bar{x} = 40.36 \pm 6.54$ m, $P = 0.58$).

In the four 100-m buffers that were intensively mapped each year, territory shifts more than doubled the mean proportion of Ovenbird territory area that occurred in zone 1, the 50-m zone immediately adjacent to the lakeside (randomization test, $P = 0.05$; Fig. 4). Once again, the contrast was more pronounced between harvested and control sites in 1997. In six 100-m buffers, the proportion of Ovenbird territory area that occurred in zone 1 ($\bar{x} = 0.37 \pm 0.09$) exceeded by more than six times the proportion recorded in the same number of control sites ($\bar{x} = 0.06 \pm 0.03$; $U = 4.0$, $P = 0.01$).

In the 200-m buffer strips, the mean minimum distance from territory boundary to riparian edge was similar in 1996 (45.58 ± 10.40 m) and 1997 (41.75 ± 10.93 m). Despite tripling after harvest, the proportion of Ovenbird area occurring in zone 1 remained low (Fig. 4). Nonetheless, the nonsignificant increase may indicate a trend.

Pairing success.—In the 100-m buffer strips, male pairing success increased from 71% ($n = 7$) to 100% ($n = 7$) after harvest. We observed the opposite effect in 200-m buffer strips, where pairing success decreased from 100% ($n = 10$) to 73% ($n = 11$). At the control sites, pairing success did not differ notably between 1996 (79%, $n = 14$) and 1997 (83%, $n = 18$). When figures from 100 m, 200 m, and control sites were combined, the overall proportion of mated males was the same before (84%, $n = 36$) and after (83%, $n = 31$) harvest. The addition of three 100-m buffer strips and one control site in the postharvest sample did not have a strong influence on estimates of pairing success (all

100-m buffers combined, 100%, $n = 14$; all controls combined, 82%, $n = 22$).

DISCUSSION

Ovenbird abundance in buffer strips.—The predicted absence of Ovenbirds from 20-m buffer strips confirms previous work in narrow riparian reserves (Stauffer and Best 1980, Triquet et al. 1990, Whitaker and Montevecchi 1999). It is also consistent with several studies that show exceptionally low abundance in small forest patches (e.g. Gibbs and Faaborg 1990, Villard et al. 1993). Ovenbird territories normally exceed 100 m in width at the narrowest point (Table 2) and will not conform to the space available in 20-m buffers. Widths of 40 to 80 m also appear to be insufficient.

In widths of 100 m, however, Ovenbird numbers were conserved in the first year after harvest. Earlier work on buffer strips in the region underscores the potential sensitivity of Ovenbirds to strip width. Working in two boreal mixed-wood buffers with average widths of 92.8 and 93.5 m, Machtans (1996) found that Ovenbirds declined in both strips following upland harvest. At the first site, parts of four Ovenbird territories occurred in the designated buffer before harvest. For two years after harvest, no territories were found. In this strip, forest widths ranged from 63 to 117 m ($\bar{x} = 92.8 \pm 3.3$ m) because buffer width was measured from the high water mark, not the tree line as in our study. At the second site, two full and two partial territories occurred in the strip before harvest, and only one full and one partial territory were present after harvest. In this strip, width of forest ranged from 75 to 119 m ($\bar{x} = 93.5 \pm 4.4$ m) except for a 100-m-long section that was 175 m wide. The widest section held the one entire territory (C. Machtans and S. Hannon unpubl. data).

Considered together, our study and that by Machtans (1996) suggest that a width of 100 m is a critical threshold for short-term conservation of Ovenbirds in boreal mixed-wood buffers. However, researchers in Maine reported no difference in Ovenbird use of an undisturbed forest along 1,000 m of lakeshore and a riparian buffer of the same length that was 70 to 100 m wide (Johnson and Brown 1990).

As predicted, 200-m buffer strips supported Ovenbird densities at preharvest levels. Postharvest crowding (i.e. increased density) did not occur in this or any other buffer width, in contrast to results for other species in buffer strips (Darveau et al. 1995) and for Ovenbirds in forest fragments (Hagan et al. 1996). The absence of a density increase suggests that remnant forests, averaging more than 80% of the land area within 800 m of lakes, absorbed individuals that were displaced from disturbed areas. Unchanging densities reduced the likelihood that territory characteristics, such as size and shape, would respond to treatments.

Territory dimensions.—Changes in territory size (i.e. decreases in 100-m and 200-m buffers concurrent with increases in their respective controls) were not statistically significant (Table 2). Without information on resource availability, it is difficult to assess the biological significance of this pattern. According to Huxley's (1934) elastic disk model, territories are compressible up to a point, beyond which resources become limiting. It is unlikely that such a point was reached in this experiment for two reasons. First, the natural variability in territory size was great in treatments and controls (Table 2). Second, territories in buffer strips (1.34 to 1.76 ha) were at the upper end of the range of sizes observed elsewhere: 0.20 to 1.80 ha in Michigan (Hann 1937), 0.61 to 1.60 ha in Ontario, and 0.88 to 1.40 ha in Missouri (Wenny 1989). Nonetheless, geographic variability in territory size, associated with differences in vegetation structure and invertebrate abundance (Stenger and Falls 1959), limits the applicability of interregional comparisons (Wiens et al. 1985).

Data on territory shape also were ambiguous. Although the circularity index showed no effect of harvest in 100- or 200-m strips, territories in 200-m buffers narrowed (Table 2). If narrowing consistently had been accompanied by elongation, the fitness of territory holders may have declined. Increased time and energy expenditure in territory defense might have limited pairing, mate guarding, and feeding opportunities (Verner 1977). However, because major territory axes showed no consistent response, we found no negative effects of territory narrowing in 200-m buffers. The narrowing observed in some 100-m buffers was even less likely to have impaired territory holders. Territory boundaries largely conformed to "hard-edged" boundaries of buffer strips, so males in 100-m buffers probably experienced low intruder pressure (Stamps et al. 1987).

Clearcut edges were not entirely impermeable. Of the 11 males occupying 100-m buffer strips, two were observed crossing clearcut boundaries. One occasionally sang in the adjacent cutblock from residual tree clumps 15 m (0.02 ha) and 65 m (0.1 ha) from the clearcut edge. Another male whose territory included an unharvested area contiguous with the buffer strip crossed the cutblock corner in two flights across approximately 150 m. In this case, a residual clump of trees served as a "stepping stone."

Territory position.—We detected no significant postharvest change in Ovenbird territory position in 200-m buffer strips. By contrast, territories in 100-m buffers shifted significantly lakeward. Considering the dimensions of Ovenbird territories, this result was predictable in the absence of gross territory compression or distortion. A sharp increase in the use of riparian edge habitat may increase the risk of brood parasitism because Brown-headed Cowbirds (*Molothrus ater*) are especially abundant at the land-water ecotone (Machtans 1996). Ovenbirds also may experience elevated interspecific competition or changes in prey availability near riparian edges. Moreover, if relocated territories contain atypical vegetation structure, they may be rejected by females that use structural cues to evaluate territory quality (Smith and Shugart 1987).

Vegetation analyses, performed at south-facing lakeshores in the same study areas (Lac La Biche and South Calling Lake), suggest that the influence of the riparian edge on canopy cover and shrub cover penetrates no more than 5 m. However, sapling density is exceptionally high up to 20 m from the edge, and the midcanopy layer is more fully developed in the zone 0 to 45 m from the edge than farther upland (K. Harper pers. comm.). This pattern corresponds with the preharvest absence of Ovenbirds from zone 1 (0 to 50 m from riparian edge). Elsewhere in Alberta, Ovenbirds are least abundant where shrubs and saplings are dense and canopy height is low (Westworth and Telfer 1993, Schieck and Nietfeld 1995). Although relocated territories may have contained some habitat that was less suitable for Ovenbirds, females continued to select mates in 100-m buffer strips.

Pairing success.—The increase in pairing success in 100-m buffers, from 71 to 100%, and the opposite pattern in 200-m strips (100 to 73%), seems counterintuitive. However, the figures were derived from small sample sizes ($7 < n < 11$). In addition, they fell symmetrically outside the range reported for Ovenbirds in northern hardwood forests, i.e. 80 to 91% (Hagan et al. 1996, King et al. 1996). When sites were pooled in each year to increase sample sizes, the overall proportion of paired males remained constant at the midpoint of the published range. Therefore, we conclude that differences resulted from chance and small sample sizes and that clearcutting did not influence pairing success in 100-m or 200-m buffer strips.

This conclusion is consistent with studies that showed no effect of timber harvest on abundance and pairing success of Ovenbirds in remnant forests (King et al. 1996, Sabine et al. 1996). However, our result contradicts observations of low pairing success associated with short-term density increases in forest fragments in a silvicultural landscape (Hagan et al. 1996). By preventing crowding, unharvested forests seem to ameliorate short-term disturbance effects on pairing success. High regional forest cover also reduces edge effects on abundance of Ovenbirds (Robbins et al. 1989, Porneluzi et al. 1993) and brood parasitism (Donovan et al. 1995, Robinson et al. 1995) and nest predation (Andrén 1995) for forest birds in general.

Research in agricultural mosaics has demonstrated that Ovenbirds have low pairing success in edge-dominated habitats (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). In our study, the lack of an effect on pairing success in 100-m buffers reinforces the distinction between agricultural and silvicultural influences on songbirds. Cotterill and Hannon (1999), Song (1998) and Song and Hannon (2000) also noted this distinction in Alberta's boreal mixed-wood forest in that no edge effects from clearcuts were apparent in studies of nest predation and avifaunal composition one to five years after harvest.

Relevance to conservation.—In extensively forested landscapes, buffers of 100 m in width seem adequate to support normally paired Ovenbirds in the short term. However, short-term data may not reflect long-term responses. In

Quebec, birds displaced from clearcut balsam fir stands crowded into remnant buffer strips in the breeding season following harvest (Darveau et al. 1995). Densities gradually declined to pretreatment levels after five years (M. Darveau pers. comm.). Determining whether our results were influenced by short-term crowding would require further postharvest study. In addition, changes in vegetation structure and composition along the clearcut edge could reduce usable habitat for Ovenbirds in buffer strips over the longer term. Direct measures of reproductive success and food availability also would enable an improved assessment of buffer suitability for Ovenbirds. Buffer strips have been shown to facilitate Ovenbird dispersal (Machtans et al. 1996) and to reduce songbird turnover in connected forest patches (Schmiegelow et al. 1997). However, the value of buffer strips cannot be fully measured without understanding their long-term suitability as reserves within the context of a dynamic forest landscape. For example, as the forest grows older and less suitable for Ovenbirds in buffers, clearcuts are regenerating and will become suitable habitat in 30 to 65 years (Westworth and Telfer 1993, Schieck and Nietfeld 1995).

Of course, it is impractical and undesirable to design buffer strips solely for Ovenbirds. However, understanding buffer-width requirements of area-sensitive species such as the Ovenbird may increase our ability to predict effects of management activities on songbirds in general. Research on the effects of different buffer-strip widths on an entire passerine assemblage up to three years postharvest is continuing as part of the TROLS program and will allow us to test the usefulness of the Ovenbird as an indicator species of landscape change in this region. In addition, bird species with large home ranges, such as raptors, will require further research on the effects of timber harvesting over larger spatial scales. Clearly, exclusive reliance on riparian reserves for wildlife conservation is inappropriate because some species may be limited to or prefer upland habitats or may require upland corridors to improve landscape connectivity. Finally, buffer widths that may conserve terrestrial wildlife may be inappropriate for the conservation of aquatic ecosystems. Hence, plans to minimize the effects of timber harvest must be developed at a landscape scale for aquatic and terrestrial wildlife.

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