

CHANGES IN BIRD COMMUNITIES IN BOREAL MIXEDWOOD FOREST: HARVEST AND WILDFIRE EFFECTS OVER 30 YEARS

KEITH A. HOBSON^{1,3} AND JIM SCHIECK²

¹Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Road,
Saskatoon, Saskatchewan, Canada S7N 0X4

²Wildlife Ecology, Forest Resources, Alberta Research Council, Vegreville, Alberta, Canada TGC 1T4

Abstract. A current paradigm in conservation biology is that forest harvest practices that better approximate natural disturbance processes are more likely to conserve biodiversity. We contrasted bird communities in three replicate stands in each of 1, 13–15, and 22–28 yr old forests following wildfire and harvest in north-central Alberta, Canada. Stands were chosen from old (>120 yr) boreal mixedwood forests having $\geq 95\%$ of the canopy trees killed during fire, and harvested sites retaining an average of 6% of the pre-harvest canopy trees. For all age classes, postharvest sites tended to have greater bird abundance. Species composition also differed between these treatment types. Two-Way Indicator Species Analysis (TWINSPAN) identified five major ecological groupings of species that differed between wildfire and harvest, and among stand ages. Correspondence analysis (CA) identified similar bird communities. Greatest differences between bird communities occurred immediately following disturbance, and gradual convergence of communities occurred throughout the first 28 yr after disturbance. Species associated with open shrub and grassland or riparian habitats were associated primarily with 1-yr postharvest stands. Three-toed Woodpeckers (*Picoides tridactyla*) and Black-backed Woodpeckers (*P. arcticus*), together with other species that use snags for foraging or nesting, occurred primarily in 1-yr postwildfire stands. Convergence in avian communities was correlated with the loss of standing snags on postwildfire sites. However, differences in bird communities were apparent up to 28 yr following disturbance, and this lack of complete convergence has important consequences for sustainable forestry practices designed to maintain biodiversity in the boreal mixedwood forest. Notably, Connecticut Warbler (*Oporornis agilis*), Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), and American Robin (*Turdus migratorius*) had higher densities on postwildfire than on postharvest stands. Lincoln's Sparrow (*Melospiza georgiana*), Alder Flycatcher (*Empidonax alnorum*), Tennessee Warbler (*Vermivora peregrina*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Mourning Warbler (*Oporornis philadelphia*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Canada Warbler (*Wilsonia canadensis*), and Pine Siskin (*Carduelis pinus*) had higher densities on postharvest stands, possibly due to the greater abundance, after harvest, of larger live residual trees and a taller and more dense shrub layer. Harvest designed to approximate stand-replacing fires may require the retention of more snags than is currently practiced. New approaches to fire salvage logging are also required to ensure adequate retention of standing dead trees on the landscape.

Key words: avian communities; boreal forest management; fire salvage; forest harvest practices; natural disturbance; TWINSPAN; vegetation structure; wildfire.

INTRODUCTION

Vegetation structure and composition are key factors determining habitat selection in birds (MacArthur and MacArthur 1961, Karr and Roth 1971, Cody 1981), and successional changes in habitats through time result in corresponding changes in bird communities (Wiens and Rotenberry 1981, James and Wamer 1982). The southern boreal mixedwood forest of western North America is a highly diverse landscape consisting of a mosaic of patches created by a series of distur-

bances, with the structure and composition of those patches changing over time (Eberhart and Woodard 1987, Johnson 1992, Lee et al. 1998). These processes have resulted in one of the richest and most diverse avifaunas of any forest type in North America (Smith 1993, Schieck et al. 1995, Kirk et al. 1996, 1997). Recently, wood extraction in this region has accelerated (Peterson and Peterson 1992, Cummings et al. 1994, Stelfox 1995) and there is concern that bird communities adapted to habitats and landscapes shaped largely by wildfire may be at risk (Welsh 1993, Monkonen and Welsh 1994, Schieck et al. 1995). These concerns have led to an interest in ecosystem management approaches to forest harvesting that may better approximate natural

Manuscript received 21 January 1998; revised 23 July 1998; accepted 6 August 1998.

³ E-mail: Keith.Hobson@ec.gc.ca

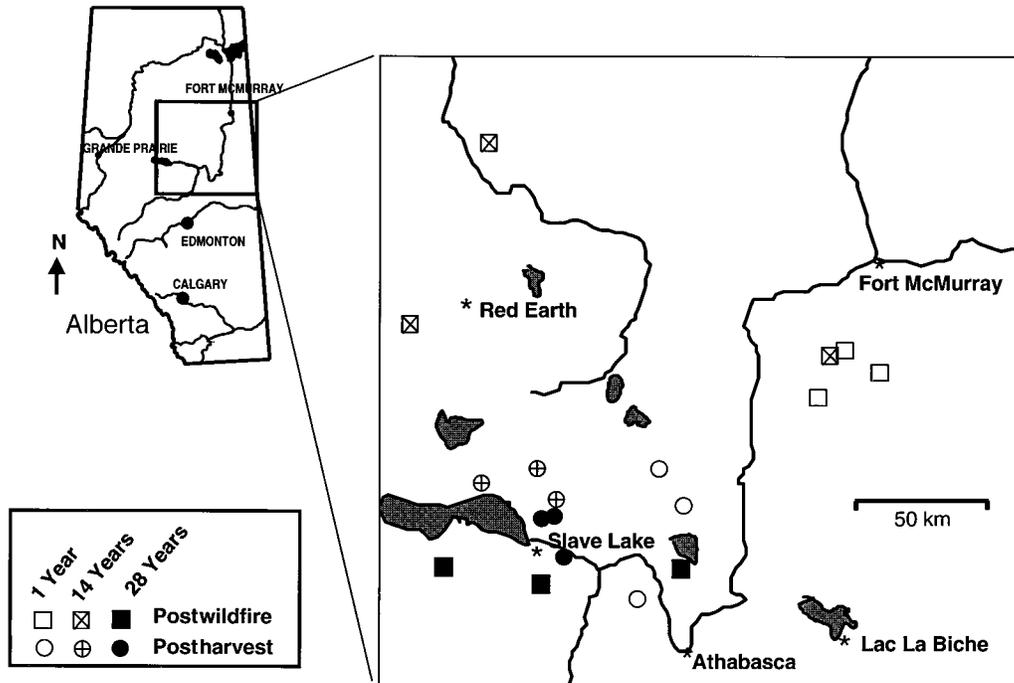


FIG. 1. Study area in north-central Alberta, depicting locations of postharvest and postfire stands.

disturbance regimes (Hunter 1993), because many early successional patches of forest will be created by forest harvesting in the future, particularly with current fire suppression (Murphy 1985, Larsen 1989).

Increasingly, there is recognition among ecologists and forest managers that retaining standing trees and associated vegetation in postharvest areas, and maintaining variation in these attributes over the landscape, may provide the only viable means by which forest harvest may be made to approximate natural disturbance (Hunter 1993, Stelfox 1995). However, at the stand level, the dispersion and abundance of standing live trees, standing dead trees (snags), downed woody material (DWM), and live understory (herbs, shrubs, saplings) remaining after harvest may not be similar to that found after wildfire (Mladenoff et al. 1993). Understanding how such differences in structural and vegetative attributes influence bird communities through forest succession is fundamental to developing harvest methods that ensure the conservation of boreal forest birds (Hunter 1993, Attiwill 1994).

Some of the initial differences between postwildfire (hereafter, postfire) and postharvest forests may disappear over time, but the rate or degree to which these two forest types, and their associated bird communities, converge during early succession is not known. Convergence may depend on the initial conditions created by fire and harvest (Johnson 1992). Previous studies in aspen (*Populus* spp.)-dominated boreal forest have indicated that most of the snags that are present following a fire decay rapidly, and that there may be little difference in snag density between postfire and post-

harvest stands as little as 25 yr after disturbance (Lee et al. 1998). However, live trees that are left after harvest continue to grow and may result in a more structurally diverse forest after harvest than after fire. Recruitment of plants into the disturbed areas also may differ between postfire and postharvest stands because soil warming and nutrient flush differ between these two types of disturbance (Peterson and Peterson 1992). We investigated how bird communities differed between postharvest and postfire stands in the mid-boreal region of Alberta. We sampled bird communities at 1 yr, 13–15 yr, and 22–28 yr after disturbance (hereafter referred to as 1-, 14-, and 28-yr age classes) to determine whether the bird communities in the two disturbance types converged. For practical purposes, we chose a retrospective analysis of existing stands of different ages rather than monitoring stands through time. However, we used aerial photos of stands taken shortly after disturbance (i.e., within 4 yr) to ensure that stands were as comparable as possible, both within and between disturbance types. We chose postfire stands having $\geq 95\%$ of the canopy trees killed during the fire and postharvest stands with an average of 6% of the pre-harvest canopy trees retained. Thus, from the perspective of standing residual trees following fire, our sites were made as comparable as possible. This study was part of a larger study investigating convergence of wildlife and vegetation following fire and harvest.

METHODS

Study sites and census methods

Our study (see Fig. 1) was conducted in the vicinities of Slave Lake (55°17' N, 114° 46' W), Red Earth Creek

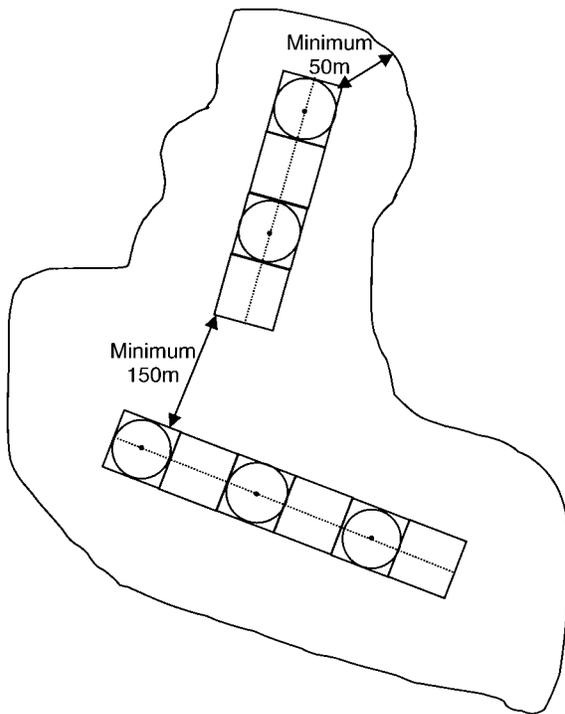


FIG. 2. Schematic representation of a typical transect and point count layout used in this study. Transects were divided into 10 1-ha units, and point counts were embedded in every second unit.

(56°33' N, 115°15' W), Calling Lake (55°13' N, 113°09' W), and Fort McMurray (56°44' N, 111°23' W) in the aspen-dominated boreal mixedwood ecoregion of Alberta, Canada (Strong and Leggat 1992). This area is a diverse mosaic of forest stand types and ages, including black spruce (*Picea mariana*), white spruce (*P. glauca*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), trembling aspen (*P. tremuloides*), white birch (*Betula papyrifera*), and numerous bogs and fens. Stands were chosen following an extensive survey of fire records, forest inventory maps, and aerial photographs. Final selection of stands was made only after stand attributes were verified on the ground. Three stands were chosen from each age class (1, 14, and 28 yr) and treatment (fire vs. harvest), for a total of 18 stands. Of all stands examined, we judged these 18 stands to best fit the following criteria. All were ≥ 50 ha (range 50–200 ha), were >5 km from other stands used in the study, and originated from old mixedwood boreal forests. For all stands, prior to disturbance, 20–50% of the canopy trees were white spruce and 50–80% were trembling aspen. We did not choose older ages, because postharvest stands >30 yr old that met our criteria were not available.

In each stand, a strip transect 100 m \times 1 km was established based on examination of aerial photos. When possible, the outer edges of the strip transects were ≥ 100 m from adjacent forest types (Fig. 2). The

shape of nine stands, however, was such that 1–32% (mean 8%) of the outer edge of the transect was 50–100 m from adjacent forest types. Bird communities were surveyed along these transects using a combination of point counts and strip transects (Verner 1985). We used both methods in order to maximize detections of forest birds. Reasoning that the conspicuousness of some species to observers would depend on the census method used, we aimed at being as inclusive as possible. Strip transects were divided into 10 1-ha sample units and permanent markers were located at the center of each unit (Fig. 2).

Birds were surveyed in each stand during four periods: once during late April and three times between 21 May and 10 July 1996. Surveys were made by five different observers, with the observers trained and methods standardized prior to conducting surveys. During each survey, the center lines of the transects were walked slowly (100 m/10 min) between sunrise and 4 h past sunrise on days with little or no wind and no rain. Locations of all birds heard or seen on the strip transects (i.e., within 50 m of the transect center line) were recorded on maps. At the center of every second 1-ha block, a 5-min point count was conducted using a 50-m detection radius, chosen because virtually all bird vocalizations could be detected at this distance, whereas that was not true for larger distances (Emlen and DeJong 1981, Wolf et al. 1995, Schieck 1997). Observers were familiar with bird vocalizations in the area. However, bird vocalizations that could not be identified were recorded using cassette tape recorders and miniparabolic microphones, and were identified later by comparison with taped vocalizations, primarily from local birds. In addition, we attempted to locate and visually identify unknown birds after the end of each survey. While conducting surveys, we attempted to record the movement of all birds onto maps so that, when these maps were summarized, each individual bird was tallied only once. Tree Swallows (see Appendix for scientific names) were detected foraging within canopy gaps and, unlike most forest birds, typically do not land in trees or on the ground while foraging (Godfrey 1986, Semenchuk 1992; but see Hobson and Sealy 1987). Consequently, we recorded them as being present when they were detected flying within 50 m of the transect center line or point count station. Other species that flew over, but did not land in a tree or on the ground, were not included in the analyses.

The order in which stands were surveyed during sampling periods was determined using a random numbers table, with the restriction that, at any given time (i.e., within ± 3 d), the same number of stands from each disturbance type and age had been surveyed. Due to safety concerns, birds were surveyed simultaneously by two observers in each stand. Observers surveyed along the transects in such a manner that they remained well spaced, by having one observer start his/her survey at the beginning of the transect and the other start

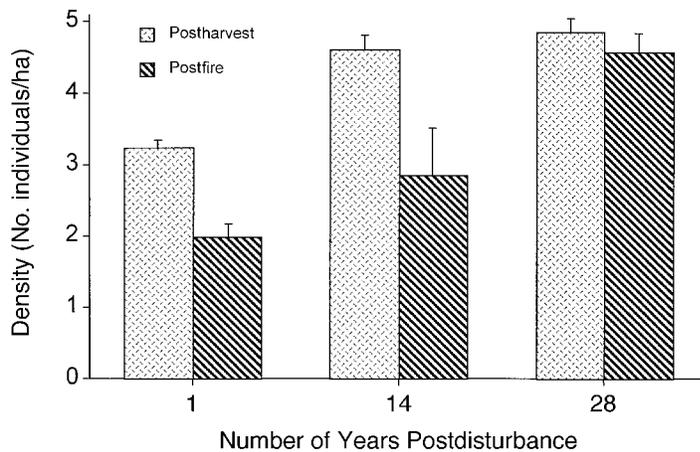


FIG. 3. Density of birds detected in mixed-wood boreal forests in Alberta at 1, 14, and 28 yr postfire and postharvest. Vertical bars denote 1 SE.

at the middle of the transect. Each observer conducted the strip transect and associated point counts; hence, each stand was completely surveyed twice during each period. Observers were rotated equally among stands.

Bird species were classified as residents based on Semenchuk (1992) and Campbell et al. (1990) and as early or late migrants based on dates when they were first observed at the Slave Lake Bird Banding Station (55°19' N, 114°46' W) and during previous bird community studies in the southern boreal forest of Alberta (C. Machtans, *unpublished data*; J. Schieck, *unpublished data*). To avoid including migrants early in the season and family groups later in the season, density estimates for resident bird species were determined based on information from the first two census periods, because many of these species were in family groups later in the season. Density estimates for early-migrant bird species were based on information from the second and third census periods, because many transient individuals were present during the first census period and some family groups were present during the fourth census. Density estimates for late-migrant bird species were determined based on information from the last two census periods, because many transient individuals were present during the first two census periods.

We summarized differences in live and dead vegetation among disturbance types and forest ages for 12 vegetation characteristics within each 1-ha unit. Within two 25 × 50 m plots, we determined the basal area of live deciduous and coniferous trees that were of pre-disturbance origin (hereafter called residual trees) and the basal area of snags that were of pre-disturbance origin (hereafter called residual snags). Within each 1-ha unit, three 25-m line transects were placed along three randomly chosen subordinal axes extending 33 m from the center of the unit. Along each of these transects, diameters of all down woody material (DWM) >5 cm were measured and volume of DWM per hectare was calculated based on the formula in Van Wagner (1968). Density and diameter at breast height (dbh) of regenerating trees were determined within one

5 × 5 m regeneration plot. Percentage of the ground surface covered by shrubs 0.5–3.0 m high and 3.1–10 m high was estimated visually within two 2 × 2 m plots. Percentage of the ground surface covered by shrubs 0–0.5-m high, herbs, grasses, and moss was estimated visually within four 0.5 × 0.5 m plots. Plots were located at random distances up to 50 m and at random directions from the center stake of each 1-ha unit.

We had multiple measures for basal areas of trees and snags, volumes of DWM, densities and dbh of regenerating trees, and percentages of the ground surface covered by shrubs, herbs, grasses, moss, litter, and nonvegetative material in each stand. It was necessary to obtain single measures for each stand, because we wished to compare vegetation characteristics and bird communities among stands. Because the distributions of the vegetation data were not normal, we summarized each vegetation characteristic as its median value for the stand (Conover 1980).

Data analyses

Because observers censused the same stand at different times during a visit, we considered each observer's census to be an independent survey of that stand. Thus, we used eight surveys (i.e., four periods with two observers) per stand in our analyses. With multiple visits to a site, breeding bird abundance can be estimated using a variety of measures (e.g., maximum, mean, median, mode) and it is not clear which measure of relative abundance is the most appropriate. Thus, we conducted analyses using maximum, mean, and the average of the maximum and minimum number of individuals recorded at a site and compared results among analyses. Arbitrarily, only those species with more than three individuals recorded over all sites were considered in our analyses. Results were considered statistically significant if the probability was <0.05 that they would occur by chance.

Correspondence analyses

Differences in bird communities between the postfire and postharvest stands and among bird communities in the three stand ages were evaluated using Correspondence Analyses (CA; ter Braak 1986, Jongman et al. 1995). To evaluate which vegetation characteristics were related to variation in the bird community types, we included the vegetation characteristics as a passive environmental data set in the CA analyses and created a biplot from the resulting scores (ter Braak 1992). Canonical Correspondence Analyses (CCA) was not used for these analyses because we wished to highlight variation in bird communities, and much of this variation might be ignored in CCA if some of the important vegetation characteristics were not included in the analyses (Halvorsen 1996). We logarithmically transformed bird species densities to give similar weights to all species (ter Braak 1992). All other CANOCO defaults were followed. We produced one CA diagram for each of the three estimates of density.

TWINSPAN analyses

Bird communities also were classified using Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979). TWINSPAN divides stands and species into smaller groups, with stand groupings based on the dissimilarity of species densities, and species groups based on the dissimilarity of their site preferences (van Tongren 1995). Because TWINSPAN uses integers for cut levels, the data sets of mean densities of species were first transformed according to $\ln(\text{mean} + 1) \times 10$. TWINSPAN analyses were conducted for each of the three density measures.

RESULTS

Species analyses

We recorded 3962 individuals from 64 species during our surveys (Appendix). Because we recorded different numbers of individuals in postharvest vs. postfire stands, we chose not to directly compare species richness among age or treatment categories (see Hagan et al. 1997). Relative abundance of birds differed significantly between disturbance types, as well as among the forest ages (two-way ANOVA: disturbance type $F_{1,16} = 9.6$, $P = 0.01$; stand age, $F_{2,16} = 11.7$, $P = 0.001$; Fig. 3). The two-way interaction was not significant in this analyses ($F_{2,14} = 1.5$, $P = 0.26$).

Patterns of change in the structure and composition of vegetation during the first 28 yr following fire and harvest differed between disturbance types (Table 1). Basal area of snags was greater in postfire stands one year following disturbance than in similar-aged postharvest stands. Within harvest stands, snag basal area did not vary significantly among ages ($F_{2,6} = 1.70$, $P = 0.261$). However, due to the rapid decline in snags after fire, the basal area of snags on postfire sites differed greatly between 1-yr and 28-yr after disturbance

($F_{2,6} = 10.04$, $P = 0.012$). In contrast, in 14-yr and 28-yr age classes, the basal area of residual standing live deciduous trees in harvested stands was greater than that for similar-aged postfire stands (Table 1). Shrubs grew more rapidly in postharvest than in postfire stands, resulting in denser shrub layers at 0.5–3 m and 3–10 m height 14 yr after disturbance (Table 1). After 28 yr, shrubs were of comparable densities among postfire and postharvest stands at 0.5–3.0 m, but still tended to be more dense on postharvest stands in the 3–10 m layer. Ground cover differed between disturbance types, and this was most notable in 1-yr-old stands, where herb cover was more common on postfire stands and grass cover more common on postharvest stands (Table 1).

Patterns of change in bird species abundance differed between disturbance types, in part because two very different bird communities were present immediately following each of the disturbance types. For example, Black-backed and Three-toed Woodpeckers and Brown Creeper occurred only on 1-yr postfire stands, whereas Clay-colored and Le Conte's Sparrows and Rusty Blackbird occurred only on 1-yr postharvest stands (Appendix). Winter Wren was found only in postfire stands and Alder Flycatcher, Common Yellowthroat, Pine Siskin, and Western Tanager were found only in postharvest stands. Those species associated strongly (but not exclusively) with postfire stands included the cavity nesters American Kestrel, Tree Swallow, and Hairy Woodpecker, and some open-cup nesting species such as American Robin, Connecticut Warbler, Gray Jay, Hermit Thrush, and Yellow-rumped Warbler. Species with much greater density in 28-yr-old postharvest than in 28-yr-old postfire stands included those typically associated with a well-developed shrub layer, such as American Redstart, Black-and-white Warbler, Canada Warbler, and Mourning Warbler.

Correspondence analysis

Data were analyzed for each of the three estimates of density. Although there were slight differences among these three sets of analyses, general patterns were similar for each. Thus, we present results for analyses based only on estimates using the maximum number of individuals of each species in each stand. We also performed ordinations using canonical correspondence analysis and detrended canonical correspondence analysis, which include the vegetation characteristics in the analyses (ter Braak 1992). Results from these additional analyses were similar to those for the CA, so we report the results of our CA analyses only.

The first correspondence function had an eigenvalue of 0.30 and accounted for 22% of the variation in bird species density. This function was negatively related to stand age, with stands 1 yr postdisturbance having high values, stands 28 yr postdisturbance having low values, and stands 14 yr postdisturbance having intermediate values (Fig. 4). This function was highly and

TABLE 1. Comparison of vegetation (mean \pm 1 SD) averaged over three treatment replicates for each age and disturbance category. Each stand value was calculated as the median of numerous plot and transect measurements.

Stand [†]	Vegetation cover (%)						Regenerating trees	
	Herb	Grass	Moss	Shrub, <0.5 m	Shrub, 0.5–3 m	Shrub, 3.1–10 m	Dbh (cm)	Density (10 ³ stems/ha)
F-01	38.0* \pm 1.3	1.3* \pm 1.0	3.7 \pm 5.5	12.2 \pm 7.3	14.8 \pm 13.2	0	0	87.8 \pm 70.0
H-01	22.1* \pm 9.5	11.7* \pm 5.8	0	16.3 \pm 7.0	22.5 \pm 9.4	0.8 \pm 1.4	0	14.7 \pm 3.8
F-14	21.0 \pm 3.8	1*	0.7 \pm 0.6	5.4* \pm 0.4	11.4* \pm 7.1	1.3 \pm 1.8	2.0* \pm 0.2	8.2 \pm 4.1
H-14	22.8 \pm 12	3.3* \pm 1.4	0	14.3* \pm 5.4	26.4* \pm 10.2	9.7 \pm 5.5	3.2* \pm 0.5	7.7 \pm 1.4
F-28	25.3 \pm 9.3	1	1.2 \pm 1.3	15.6 \pm 5.9	26.4 \pm 10.1	3.8 \pm 3.9	5.9 \pm 0.3	5.5* \pm 0.9
H-28	17.9 \pm 6.9	1	0	13.7 \pm 3.3	20.0 \pm 5.4	10.5 \pm 5.6	5.4 \pm 0.3	2.1* \pm 0.5

* Significant difference between harvest and fire treatment for each category ($P < 0.05$, t test for samples with unequal variance).

[†] F designates postfire stands and H designates postharvest stands, followed by the number of years after disturbance.

[‡] DWM = down woody material.

positively correlated with basal area of residual snags and density of regenerating trees, and was highly and negatively correlated with dbh of regenerating trees and density of shrubs 3–10 m. (Fig. 4). The second function from the correspondence analyses had an eigenvalue of 0.23 and explained 17% of the variation in bird species density. This function (Fig. 4) separated stands 1 yr postharvest (high values on CA2), stands 14 and 28 yr postharvest and postfire (moderate values), and stands 1 yr postfire (low values). Stands 14 and 28 yr postharvest tended to have higher values on this second function than stands 14 and 28 yr postfire, but that difference was not great (Fig. 4). This function was highly and positively correlated with percentage of grass cover and volume of DWM (Fig. 4).

To evaluate whether bird communities differed statistically between consecutive age classes within each disturbance type or between disturbance types at each of the age classes, we coded treatment groups as dummy variables and included them as the only environmental variables in a CCA analyses (ter Braak 1992). Differences found in these analyses are described qualitatively based on Fig. 4, and more quantitatively in the TWINSPAN section. Within postfire stands, bird communities differed among each of the three age classes, whereas within postharvest stands, bird communities differed between stands 1 yr and 14 yr after harvest, but not between stands 14 and 28 yr postharvest (Table 2). Bird communities within stands 1 yr and 14 yr postfire differed from those within stands 1 yr and 14 yr postharvest, respectively. However, bird communities within stands 28 yr postfire were not statistically different from those within stands 28 yr postharvest (Table 2).

We included bird species on the biplot of our CA to associate each species with the confidence ellipses from each stand age and disturbance type (Fig. 5). As expected, those bird species with relatively high density in early postfire stands (Table 3) had their predicted maximum densities within the trajectory defined by postfire stands (i.e., within or between the confidence ellipses for the postfire stands (Fig. 5). Species with

relatively high density in postharvest stands (Table 3) had their predicted maximum densities within the trajectory for the postharvest stands (Fig. 5). Black-backed Woodpecker and Brown Creeper, species detected only within 1-yr-old postfire stands, had their predicted maximum density close to the center of the 67% confidence ellipse for these stands. Similarly, those species detected only within 1 yr postharvest stands, Le Conte's Sparrow, Rusty Blackbird, and Fox Sparrow, had their predicted maximum densities within the ellipse associated with that treatment type. Winter Wren, American Kestrel, and Hairy Woodpecker had higher densities postfire than postharvest (Table 3) and occurred at intermediate positions along the postfire trajectory. Within the 14- and 28-yr-old stands, trajectories converged between disturbance types, and species that had their predicted maximum in these stands had more overlap between treatment types. Some species (Yellow-bellied Sapsucker, Mourning Warbler, Swamp Sparrow, Ovenbird, and Warbling Vireo) had considerable overlap between treatment types (Appendix). Other species (Downy Woodpecker, Yellow-rumped Warbler, Gray Jay, Blue-headed Vireo, White-throated Sparrow, Tree Swallow, Pileated Woodpecker, Black-capped Chickadee, American Robin, and Hermit Thrush) had greater density within 14-yr-old postfire stands than in postharvest stands (Appendix). Two species, Magnolia Warbler and Connecticut Warbler, had high density in stands 28 yr postfire (Appendix). Several species (e.g., American Redstart, Yellow Warbler, Black-and-white Warbler) had their highest density in stands 28 yr postharvest and were strongly associated with a well-developed shrub layer.

TWINSPAN analysis

TWINSPAN provided additional insights into the way both stands (Table 4) and species (Table 3) could be aggregated. At the first level of classification, TWINSPAN separated all three 1 yr postfire stands and a single 14 yr postfire stand (F14-3) from all others. At the second level, all of the 1-yr-old postharvest stands were separated from the larger group of postfire

TABLE 1. Extended.

Basal area of residual trees (m ² /ha)			Volume DWM [†] (m ² /ha)
Deciduous	Coniferous	Snag	
0*	0*	35.5* ± 8.5	232* ± 42
2.5* ± 1.5	0.3* ± 0.2	1.9* ± 0.8	464* ± 75
1.5* ± 1.8	0.13 ± 0.22	9.7* ± 4.2	322 ± 42
5.9* ± 0.5	0.5 ± 0.6	3.0* ± 1.8	281 ± 56
0.1* ± 0.2	0.01 ± 0.01	2.5 ± 1.2	291 ± 20
4.5* ± 1.5	0.26 ± 0.22	5.1 ± 3.1	318 ± 42

and postharvest stands. At the third level, the remaining 14-yr-old postfire stands (F14-1, F14-2) were separated from the large group. At the fourth level, TWINSpan separated all of the 14-yr-old harvest stands and a single 28-yr-old harvest stand (H28-2) from the two 28-yr-old postharvest stands and all of the 28-yr-old postfire stands. Only at the fifth level did TWINSpan separate the three 28-yr-old postfire stands from the remaining 28-yr-old postharvest stands.

TWINSpan identified five major groups of bird spe-

TABLE 2. Tests for differences in bird communities among ages and disturbance types of mixedwood boreal forests in Alberta.

Comparison type	N [†]	F	P
Postfire all ages	3	2.54	<0.001
Postharvest all ages	3	2.44	<0.001
Postfire 1 vs. postfire 14	2	2.27	<0.001
Postfire 14 vs. postfire 28	2	1.85	<0.001
Postharvest 1 vs. postharvest 14	2	2.67	<0.001
Postharvest 14 vs. postharvest 28	2	1.32	0.24
Postfire 1 vs. postharvest 1	2	2.67	<0.001
Postfire 14 vs. postharvest 14	2	1.79	<0.001
Postfire 28 vs. postharvest 28	2	1.56	0.11

Notes: Tests were conducted using a bootstrap Monte Carlo procedure in a canonical correspondence analyses, with treatment types coded as dummy variables and included as the only environmental variables (ter Braak 1992).

[†] The number of stand types compared in the analyses.

cies after the third level of division (Table 3). At the first division, groups A, B, and C were split from groups D and E (TWINSpan groups are identified in Table 3). At the second division, group C was split from groups A and B, and group D was split from group E.

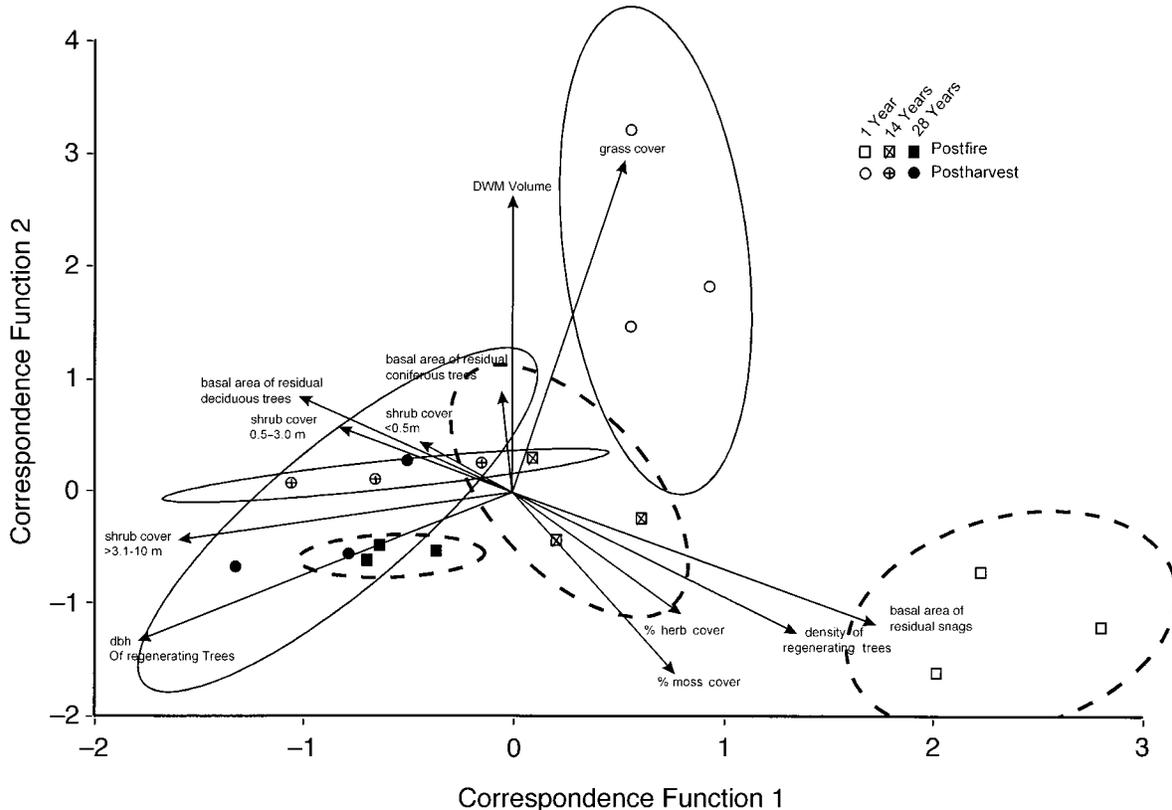


FIG. 4. Two dimensional bi-plot depicting how environmental variables varied in the correspondence analyses (CA) involving bird communities from mixedwood boreal forests in Alberta at 1, 14, and 28 yr postfire and postharvest. Stands that are close together have similar bird communities, and stands far apart have different bird communities. We present 67% confidence ellipses (postfire and postharvest with dotted lines and solid lines, respectively), because these give similar results to the bootstrap Monte Carlo test presented in the text. Vegetation variables are included as passive variables in this analysis. Arrows indicate the direction and magnitude of increase for the vegetation characteristics.

TABLE 3. Tests evaluating whether species density differed between disturbance (postfire vs. postharvest) and stand age (1, 14, 28 yr) in mixedwood boreal forests in Alberta. Results are presented (in boldface, if statistically significant) for the chi-squared approximation of the Wilcoxon test and a Kruskal-Wallis test for disturbance and age categories, respectively.

Species† (no. observations)	Code	TWIN- SPAN group	Forag- ing guild‡	Nest site§	Nest type	Treatment effects			Age effects		
						Highest density¶	Sta- tistic	P	Highest density#	Sta- tistic	P
Cedar Waxwing (13)	CEWA	A	FI	C	O	H	2.8	0.09	1	0.4	0.8
Yellow-bellied Sapsucker (27)	YBSA	A	BI	C	CV	H	0.4	0.53	28	1.4	0.5
Alder Flycatcher (24)	ALFL	A	AI	S	O	H	23.7	<0.001	14	0.3	0.86
Common Yellowthroat (26)	COYE	A	FI	S	O	H	23.7	<0.001	1	0.5	0.77
Fox Sparrow (4)	FOSP	A	GI	G	O	H	2.0	0.16	1	2.0	0.37
Le Conte's Sparrow (25)	LCSP	A	FI	G	O	H	20.5	<0.001	1	4.2	0.12
Mourning Warbler (128)	MOWA	A	FI	G	O	H	63.4	<0.001	1	0.2	0.92
Pine Siskin (12)	PISI	A	OM	C	O	H	9.1	0.02	1	1.6	0.45
Rusty Blackbird (4)	RUBL	A	OM	S	O	H	3.1	0.08	1	6.8	0.03
Western Tanager (4)	WETA	A	FI	C	O	H	3.0	0.08	28	2.3	0.32
Swamp Sparrow (9)	SWSP	A	OM	S	O	H	0.5	0.48	14	1.9	0.39
Chipping Sparrow (36)	CHSP	A	FI	S	O	H	2.8	0.10	1	4.6	0.1
Lincoln's Sparrow (96)	LISP	A	FI	G	O	H	47.5	<0.001	1	4.5	0.11
Red-breasted Nuthatch (34)	RBNU	A	BI	C	CV	H	2.4	0.12	28	1.5	0.47
Tennessee Warbler (402)	TEWA	A	FI	S	O	H	15.1	<0.001	14	10.5	0.01
Least Flycatcher (17)	LEFL	B	AI	S	O	F	3.4	0.07	28	1.3	0.53
Black-and-white Warbler (64)	BWWA	B	FI	G	O	H	13.7	0.02	28	8.8	0.01
Magnolia Warbler (7)	MAWA	B	FI	S	O	F	2.7	0.1	28	2.1	0.34
Red-eyed Vireo (159)	REVI	B	FI	C	O	H	1.0	0.32	14,28	9.8	0.01
Swainson's Thrush (26)	SWTH	B	GI	S	O	ND	0.0	0.01	14,28	10.1	0.01
Warbling Vireo (5)	WAVI	B	FI	C	O	H	1.8	0.18	28	2.4	0.3
Yellow Warbler (18)	YWAR	B	FI	S	O	H	10.2	0.01	14	4.2	0.12
American Redstart (163)	AMRE	B	FI	S	O	H	103.7	<0.001	28	7.6	0.02
Blue Jay (12)	BLJA	B	OM	C	O	H	2.8	0.09	14,28	3.6	0.17
Canada Warbler (52)	CAWA	B	FI	G	O	H	28.9	<0.001	28	5.8	0.05
Rose-breasted Grosbeak (39)	RBGR	B	FI	C	O	H	19.8	<0.001	14	12.9	0.00
Ovenbird (146)	OVEN	B	FI	G	O	H	1.2	0.27	28	14.2	0.00
Connecticut Warbler (17)	COWA	B	FI	G	O	F	10.2	0.01	28	2.8	0.25
Ruffed Grouse (54)	RUGR	B	OM	G	O	H	3.0	0.08	14,28	11.0	0.00
Black-capped Chickadee (104)	BCCH	C	OM	C	CV	F	1.1	0.29	14,28	7.9	0.02
Philadelphia Vireo (14)	PHVI	C	FI	C	O	F	0.3	0.60	14,28	8.9	0.01
American Robin (36)	AMRO	C	GI	S	O	F	9.6	0.02	14	1.1	0.59
Common Raven (14)	CORA	C	OM	C	O	F	0.1	0.76	1,28	6.3	0.04
Hermit Thrush (42)	HETH	C	GI	S	O	F	6.2	0.01	14	8.1	0.02
Downy Woodpecker (6)	DOWO	C	BI	C	CV	F	1.8	0.18	14	4.3	0.12
Pileated Woodpecker (7)	PIWO	D	BI	C	CV	H	0.1	0.7	14	4.4	0.11
Hairy Woodpecker (27)	HAWO	D	BI	C	CV	F	4.0	0.04	1	4.4	0.11
Black-backed Woodpecker (9)	BBWO	D	BI	C	CV	F	8.1	0.04	1	6.8	0.03
Brown Creeper (15)	BRCR	D	BI	C	CV	F	12.2	0.01	1	6.8	0.03
Gray Jay (26)	GRJA	D	OM	C	O	F	7.3	0.05	14	3.7	0.16
Winter Wren (8)	WIWR	D	GI	G	CV	F	8.1	0.04	1	0.6	0.74
American Kestrel (18)	AMKE	D	CA	C	CV	F	5.5	0.02	1	7.1	0.03
Tree Swallow (35)	TRSW	E	AI	C	CV	F	10.3	0.01	14	0.4	0.82
White-throated Sparrow (436)	WTSP	E	FI	G	O	F	1.0	0.32	28	1.0	0.61
Common Snipe (6)	COSN	E	GI	G	O	H	0.7	0.41	1	4.2	0.12
Dark-eyed Junco (33)	DEJU	E	OM	G	O	H	3.2	0.07	1	2.4	0.31
Northern Flicker (51)	NOFL	E	BI	C	CV	F	2.5	0.12	14	4.5	0.11
Orange-crowned Warbler (15)	OCWA	E	FI	S	O	F	0.8	0.37	14	6.8	0.03
Yellow-rumped Warbler (99)	YRWA	E	FI	C	O	F	2.4	0.13	1	1.2	0.55

† Species are grouped based on nesting and foraging habitats and are presented in arbitrary order within their TWINSpan groupings.

‡ Key: FI, foliage insectivore; BI, bark insectivore; GI, ground insectivore; CA, carnivore; OM, omnivore.

§ Key: G, on ground; C, in large canopy tree; S, in shrubs, saplings, or understory trees.

|| Key: O, open cup; CV, cavity or hole.

¶ Stand type in which species reached greatest density: H, postharvest; F, postfire; ND, no difference between postharvest and postfire.

Age of stand after disturbance (in years) in which species reached greatest density.

TABLE 4. TWINSPAN groupings of stands. Stands are denoted by a code that signifies fire (F) or harvest (H), the age of the stand (1-, 14-, and 28-yr), and the replicate number (1, 2, or 3).

TWINSpan group	Stands
1	H1-1, H1-2, H1-3
2	H28-2, H14-1, H14-2, H14-3
3	H28-1, H28-3
4	F28-1, F28-2, F28-3
5	F14-1, F14-2
6	F14-3, F1-1, F1-2, F1-3

ticularly in western North America, where avian communities have adapted to stand age and composition changes following disturbance by fire (Westworth and Telfer 1993, Schieck et al. 1995, Kirk et al. 1996).

Bird communities in 1-yr postfire stands were dominated by species that nest and forage in large snags, and included two species, Black-backed and Three-toed Woodpeckers, known to be strongly associated with young postfire habitats (Bock and Bock 1974, Short 1982, Hutto 1995). In contrast, the bird community present in 1-yr postharvest stands included species that typically nest and forage in open grass or shrubby habitats (e.g., LeConte's Sparrow, Clay-colored Sparrow, Common Yellowthroat, Rusty Blackbird, Common Snipe), probably because those areas had many residual trees dispersed among open grassy areas where the trees had been harvested. Westworth and Telfer (1993) and Kirk et al. (1996) similarly found that Le Conte's and Clay-colored Sparrows had their highest density in clearcuts in aspen-dominated forests of western Canada. Norton and Hannon (1997) also found that those species that gained in harvested sites in boreal mixed-wood forest of northern Alberta were mostly birds of open or shrubby habitats. Freedman et al. (1981) included Common Yellowthroat among the most common species in clear-cut plots in Nova Scotia.

The large initial differences in bird communities between postfire and postharvest stands diminished by 14 yr after disturbance. That convergence was due to: open-habitat species having lower densities in 14- than in 1-yr-old postharvest stands; bird species that specialize on large dead trees having lower densities in 14- than in 1-yr-old postfire stands; and those species that nest and forage in shrubs (e.g., Orange-crowned Warbler, Swamp Sparrow) having higher densities in 14- than in 1-yr-old stands following both disturbance types. Convergence in bird communities may have occurred because the forest structure converged during that same period. Many standing dead trees were present immediately following fire, although their abundance decreased rapidly during the first decade as snags blew down. Postharvest sites lacked the initial abundance of standing dead trees, although they slowly produced snags from standing live residual trees through time (Peterson and Peterson 1992). Distinct differ-

ences, however, remained between 14-yr-old postfire and postharvest bird communities. A few bird species that nest and forage in large snags (e.g., Hairy Woodpecker, Northern Flicker, Alder Flycatcher, Tree Swallow) had higher densities in 14-yr-old postfire than in 14-yr-old postharvest stands, possibly due to the higher density of large snags that remained in postfire stands. In addition, a few bird species that nest or forage in closed-canopy forests (e.g., Rose-breasted Grosbeak, Pileated Woodpecker, Black-capped Chickadee; see Westworth and Telfer 1993, Schieck et al. 1995, Kirk et al. 1996) had higher density in 14-yr-old postharvest than in 14-yr-old postfire stands, possibly due to the presence of live canopy trees that were retained and continued to grow in the harvested areas. Postfire stands had few large, live residual trees.

Convergence in bird communities continued during the period between 14 and 28 yr after disturbance. Much of that convergence, however, was due to changes within the postfire bird community, because bird communities were similar between forests 14 and 28 yr after harvest. Bird species that nest and forage in large snags had lower density in 14- than in 28-yr-old postfire stands, whereas those species typically requiring a more developed shrub layer (e.g., White-throated Sparrow, Mourning Warbler, Connecticut Warbler, Black-and-white Warbler; see Kirk et al. 1996) had higher density. Postharvest stands had a more rapid shrub regeneration than did postfire stands, and shrub dominance was maintained over postfire stands even after 28 yr.

The absence of complete convergence in bird communities after 28 yr following disturbance may be related to differences in shrub density or vertical structure, amount of ground cover, and abundance of large, live residual canopy trees. Our 28-yr-old postharvest stands may have been structurally more typical of older postfire stands, because species associated with old aspen-dominated stands in western Canada (e.g., American Redstart, Canada Warbler, Black-and-white Warbler) had higher densities there (see Schieck et al. 1995, Kirk et al. 1996). Unfortunately, detailed habitat requirements of most boreal forest birds are poorly known, and previous studies in this area have typically contrasted species density among broader forest age

TABLE 5. Number of species in each nesting substrate and type within each TWINSpan group. The proportion of the total group is given in parentheses.

TWINSpan group	Open nesters			Cavity nesters
	On ground	In shrub strata	In canopy tree	In canopy tree
A	4 (0.27)	6 (0.40)	3 (0.20)	2 (0.13)
B	4 (0.31)	4 (0.31)	5 (0.39)	0
C	0 (0)	2 (0.33)	2 (0.33)	2 (0.33)
D	0	0	1 (0.14)	6 (0.86)
E	3 (0.43)	1 (0.14)	1 (0.14)	2 (0.29)

class distributions and vegetation chronosequences than the relatively short period examined in our study (but see Kirk et al. 1996).

For some species, it was not clear which habitat features resulted in differential use of postfire and postharvest stands. In contrast to Mourning Warblers, which had high densities in 28-yr-old postharvest stands, Connecticut Warblers had high densities in 28-yr-old postfire stands. Previous studies in aspen-dominated forests of western Canada (Westworth and Telfer 1993, Schieck et al. 1995, Kirk et al. 1996) suggest that, although both species reach high densities in young forests, Mourning Warblers have their highest abundance in older stands than do Connecticut Warblers. The separation of these species in our study was consistent, with our postharvest stands having a more advanced shrub component and more residual live trees than the postfire stands of similar age. Connecticut Warblers may favor the simpler shrub layer typical of earlier successional stages, or, as ground nesters, they may have fairly specific ground cover requirements. However, habitat affinities described for this species differ considerably throughout its range (Welsh 1993, Kirk et al. 1996, Welsh and Loughheed 1996).

We found that the Chipping Sparrow and Dark-eyed Junco were most common in young postharvest stands. Elsewhere in the region, these species have been associated with mature aspen and mixedwood stands (Kirk et al. 1996), although Hutto (1995) associated both species with early postfire stands in conifer-dominated forests of the northern Rocky Mountains (see also Hansen et al. 1995). Similarly, the Yellow-rumped Warbler, a species previously associated with conifer-dominated mixedwoods, had its highest density on young postfire stands in our study. Hutto (1995) also associated Yellow-rumped Warblers with early- and mid-succession burned forest in mountain conifer forests. Within young successional forests, some species may be less associated with a particular successional stage or treatment and more associated with selected microhabitats (see Welsh 1987, Kirk et al. 1996). In our study, Swainson's Thrush, Swamp Sparrow, and Warbling Vireo showed little affinity to any age or disturbance type, and may well have required habitat features common to both postfire and postharvest stands. Both Swainson's Thrush and Ovenbird have been associated with older, closed-canopy forests elsewhere (e.g., Erskine 1977, Welsh 1987, Hansen et al. 1995, Kirk et al. 1996), but their occurrence in forests as young as 14 yr old suggests plasticity in their use of disturbed habitats. Information is required to evaluate which habitat features allow these older closed-canopy forest specialists to persist in younger stands following harvest. In addition, little is known about the reproductive success of older forest specialists in these younger stands.

We did not survey the total spectrum of forests that are present postfire and postharvest, and thus the bird

communities that we found may not represent the total spectrum of bird communities that are present following those disturbances (Hutto 1995, Kirk et al. 1996). The areas that we surveyed had >50 ha of mixedwood forests that had burned, and were restricted to those areas where fires killed >95% of the trees. Similarly, our postharvest surveys were restricted to areas where many snags and 6% of the pre-harvest canopy trees had been retained at harvest. Retention of >6% of the pre-harvest canopy trees may increase the density of forest birds that nest and forage in large trees or that require understory characteristics promoted by the presence of canopy trees (Norton and Hannon 1997). However, major companies operating in the southern boreal mixedwood forest of western Canada currently retain <1% of the trees as standing residuals after harvest.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Many authors have suggested that conservation of biota in temperate forests managed for extraction of wood products will probably be achieved only through the adoption of management practices that approximate natural disturbance events (Hunter 1993, Bunnell 1995, Stelfox 1995, DeLong and Tanner 1996). This appears to be particularly true for boreal forest bird communities that have adapted to natural seral stages with distinct suites of structural attributes (Hansen et al. 1991, 1995, Westworth and Telfer 1993, Schieck et al. 1995, Welsh and Loughheed 1996). An important component of stand structure following disturbance is the amount and orientation of residual live and dead trees. In our study, we were able to contrast sites with similar densities and distributions of standing live trees, but very different amounts of standing dead trees. Postfire stands consisted initially of mostly standing dead trees, whereas postharvest stands included primarily clumps of standing live trees. This difference accounted for much of the initial differences in bird communities.

Black-backed Woodpecker, Three-toed Woodpecker, Hawk Owl, and potentially Hairy Woodpecker, probably require high snag densities (Raphael and White 1984, Raphael et al. 1987, Hutto 1995) and will be of management concern if few postfire forests remain on the landscape. Suitable densities of nesting cavities might be maintained for these and other cavity nesters through modified harvesting techniques. Industrial forestry, however, does not currently provide the high levels of snags and their associated wood-boring insect prey that are present in early postfire stands. It is not possible to modify forest harvest practices to produce the abundance of snags that are found after natural disturbance events. As such, the maintenance of suitable amounts of postfire forests that are spared from commercial salvage logging is recommended (Hutto 1995). Postfire habitats, however, may become rarer on the landscape as a consequence of fire suppression. In

addition, average stand ages will be reduced through short-rotation forest management practices, with the consequence that future postfire stands may not resemble those present under a natural disturbance regime. Future studies are required to evaluate whether postharvest stands that burn are similar to natural stands that burn. In addition, managers require information on the threshold amounts and types of standing dead trees for snag-dependent species. Finally, little is known about how these burned areas should be distributed over the landscape to maintain adequate populations of species that historically relied on early postfire habitats.

Other species not necessarily associated with snags also may be of management concern as more and more of the landscape becomes modified by harvest and less is disturbed by fire. For example, relatively low densities of Connecticut Warblers, Hermit Thrushes, Magnolia Warblers, and Gray Jays were found in postharvest compared with postfire stands. These species may be responding to differences in the herb and shrub strata between postharvest and postfire stands. These bird species, however, being found in many forest types (e.g., Kirk et al. 1996), probably are of less management concern than snag-dependent birds.

For some species of birds, it may be possible to make at least part of a postharvest stand more similar to that found after fire by burning, or otherwise killing, some of the clumps of residual trees that remain after harvest (Hutto 1995). However, there are management trade-offs between killing vs. retaining residual live trees in postharvest stands, because those residual trees, if left alive, will grow and produce large live and dead trees in mid- and late-rotation stands. Large live and dead trees, especially if they are in clumps, may produce the forest structures and microclimates that otherwise would not be present in landscapes managed for wood products. If old forests become rare in landscapes as a consequence of forest harvest, then forest management to accelerate some characteristics and structures that normally are found in old growth may be needed (Schieck et al. 1995).

Overall, the most dramatic differences in bird communities between postharvest and postfire stands occurred immediately following the disturbances. If managers wish to pattern harvest in the boreal forest based on a natural disturbance regime, then strategies to compensate for these initial differences must be developed and implemented. That remains a major challenge at present.

ACKNOWLEDGMENTS

This research was part of a larger study on the effect of fire and timber harvest residuals on biodiversity and forest stand/landscape structure in mixedwood communities in Alberta, conducted by the Alberta Research Council. Phil Lee and Susan Crites designed and supervised collection of the vegetation data used in this paper. Len Peleshok, Dave McKinnon, Liz Joyce, Selena Cole, Kelley Sturgess, Debby Franchuk, and Kristi Anderson helped to collect, enter and check the data. This project was generously supported by the

Alberta Research Council, Alberta-Pacific Forest Industries, Daishowa-Marubeni International, Forestry Canada, Canadian Wildlife Service, and the Alberta Forest Service. C. Machtans assisted with data analysis and reviewed earlier versions of the manuscript. We thank the Lesser Slave Lake Bird Observatory for use of their migration monitoring data.

LITERATURE CITED

- Attiwill, P. M. 1994. Disturbance of forest ecosystems: the ecological basis for conservation management. *Forest Ecology and Management* **63**:247–300.
- Bock, C. E., and J. H. Bock. 1974. On the geographical ecology and evolution of the Three-toed woodpeckers, *Picoides tridactylis* and *P. arcticus*. *American Midland Naturalist* **92**:397–405.
- Bunnell, F. L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia. *Conservation Biology* **9**:636–644.
- Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper., G. W. Kaiser, and M. C. McNall. 1990. Birds of British Columbia. Volume II. Royal British Columbia Museum, Victoria, British Columbia, Canada.
- Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors and productivity. *BioScience* **31**:107–113.
- Conover, W. J. 1980. Practical nonparametric statistics. Second edition. John Wiley, Toronto, Ontario, Canada.
- Cummings, S. G., P. J. Burton, S. Prahacs, and M. R. Garland. 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: a simulation study. *Forest Ecology and Management* **68**:281–302.
- DeLong, S. C., and D. Tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiversity and Conservation* **5**:1191–1205.
- Eberhart, K. E., and P. M. Woodard. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* **17**:1207–1212.
- Emlen, J. T., and M. J. DeJong. 1981. The application of song detection threshold distance to census operations. Pages 346–352 in C. J. Ralph and M. Scott, editors. Estimating numbers of terrestrial birds: Proceedings of an International Symposium held at Asilomar, California. Studies in Avian Biology. Volume 6. Cooper Ornithological Society, Los Angeles, California, USA.
- Erskine, A. J. 1977. Birds in boreal Canada: communities, densities and adaptations. Canadian Wildlife Service Report Series Number 41, Ottawa, Ontario, Canada.
- Freedman, B., C. Beauchamp, I. A. McLaren, and S. I. Tingley. 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. *Canadian Field-Naturalist* **95**:307–311.
- Godfrey, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa, Ontario, Canada.
- Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance in a northeastern industrial forest. *Journal of Wildlife Management* **61**:718–735.
- Halvorsen, O. R. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science* **7**:289–292.
- Hansen, A. J., W. C. McComb, R. Vega, M. Raphael, and M. Hunter. 1995. Bird habitat relationships in natural and managed forests in the west cascades of Oregon. *Ecological Applications* **5**:555–569.
- Hansen, A. J. T., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity on managed forests. Lessons from natural forests. *BioScience* **41**:382–392.
- Helle, P., and M. Monkkonen. 1990. Forest successions and bird communities: theoretical aspects and practical implications. Pages 299–318 in A. Keast, editor. Biogeography

- and ecology of forest bird communities. S.P.B. Academic Publishing, The Hague, The Netherlands.
- Hill, M. O. 1979. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University Press, Ithaca, New York, USA.
- Hobson, K. A., and S. G. Sealy. 1987. Foraging, scavenging and other behavior of swallows on the ground. *Wilson Bulletin* **99**:111–116.
- Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* **65**: 115–120.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* **9**:1041–1058.
- James, F. C., and N. O. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* **63**:159–171.
- Johnson, E. A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, UK.
- Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.
- Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* **105**:423–435.
- Kirk, D. A., A. W. Diamond, K. A. Hobson, and A. R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Canadian Journal of Zoology* **74**:1749–1770.
- Kirk, D. A., A. W. Diamond, A. R. Smith, G. E. Holland, and P. Chytky. 1997. Population changes in boreal forest birds in Saskatchewan and Manitoba. *Wilson Bulletin* **109**: 1–27.
- Larsen, C. P. S. 1989. Fire resolution paleoecology in the boreal forest of Alberta: a long-term record of fire-vegetation dynamics. Thesis. McMaster University, Hamilton, Ontario, Canada.
- Lee, P. C., S. Crites, M. Nietfeld, H. V. Nguyen, and J. B. Stelfox. 1998. Characteristics and origin of deadwood material in aspen-dominated boreal forests. *Ecological Applications* **7**:691–701.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594–598.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial patterns in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* **3**: 294–306.
- Monkonen, M., and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Annales Zoologici Fennici* **31**:61–70.
- Murphy, P. J. 1985. History of forest and prairie fire control policy in Alberta. Report T/77. Alberta Energy and Natural Resources, Edmonton, Alberta, Canada.
- Norton, M. R., and S. J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research* **27**:44–53.
- Peterson, E. B., and N. M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Special Report 1, Edmonton, Alberta, Canada.
- Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. *Condor* **89**: 614–626.
- Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* **86**:1–66.
- Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. *Condor* **99**:179–190.
- Schieck, J., M. Nietfeld, and J. B. Stelfox. 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. *Canadian Journal of Zoology* **73**:1417–1431.
- Semenchuk, G. P. 1992. The atlas of breeding birds of Alberta. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.
- Short, L. L. 1982. Woodpeckers of the world. Monograph Series Number 4. Delaware Museum of Natural History, Greenville, Delaware, USA.
- Smith, A. 1993. Ecological profiles of birds in the boreal forest of western Canada. Pages 27–38 in H. Kuhnke, editor. *Birds in the boreal forest*. Forestry Canada Northwest Region, Northern Forestry Centre, Edmonton, Alberta, Canada.
- Stelfox, B. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre, Vegreville and Canadian Forest Service, Edmonton, Alberta, Canada.
- Strong, W., and K. R. Leggat. 1992. Ecoregions of Alberta. Resource Information Branch Publication Number T:245. Alberta Forestry, Lands, and Wildlife, Edmonton, Alberta, Canada.
- ter Braak, C. J. 1986. Canonical correspondence analyses: a new eigenvector technique for multivariate direct gradient analyses. *Ecology* **67**:1167–1179.
- . 1992. CANOCO—A FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca, New York, USA.
- van Tongeren, O. F. R. 1995. Cluster analysis. Pages 174–212 in R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, editors. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, UK.
- Van Wagner, C. E. 1968. The line intersect method for forest fuel sampling. *Forest Science* **14**:20–26.
- Verner, J. 1985. Assessment of counting techniques. Pages 247–301 in R. F. Johnston, editor. *Current Ornithology Volume 2*. Plenum, New York, New York, USA.
- Welsh, D. A. 1987. The influence of forest harvesting on mixed coniferous-deciduous boreal bird communities in Ontario, Canada. *Acta Oecologia/OEcol. Gener.* **8**:247–252.
- . 1993. Birds and boreal forests in Ontario. Pages 40–47 in H. Kuhnke, editor. *Birds in the boreal forest*. Forestry Canada Northwest Region, Northern Forestry Centre, Edmonton, Alberta, Canada.
- Welsh, D. A., and S. C. Lougheed. 1996. Relationships of bird community structure and species distributions to two environmental gradients in the northern boreal forest. *Ecography* **19**:194–208.
- Westworth, D. A., and E. S. Telfer. 1993. Summer and winter bird populations associated with five age classes of aspen in Alberta. *Canadian Journal of Forest Research* **23**:1830–1836.
- Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* **51**:21–41.
- Wolf, A. T., R. W. Howe, and G. J. Davis. 1995. Detectability of forest birds from stationary points in northern Wisconsin. Pages 19–23 in C. J. Ralph, J. R. Sauer, and S. Droege, editors. *Monitoring bird populations by point counts*. U.S. Forest Service General Technical Report **PSW-GTR-149**.

APPENDIX

Index of density for each of the bird species detected during surveys within three ages of postfire and postharvest mixedwood boreal forest in Alberta, Canada. Densities are presented as mean (± 1 SE) number of individuals/10 ha.

Species	Migration category†	Number of years postfire			Number of years postharvest		
		1	14	28	1	14	28
Mallard (<i>Anas platyrhynchos</i>)	E	0.0 \pm 0.0	1.0 \pm 1.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Cinnamon Teal (<i>Anas cyanoptera</i>)	E	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.7 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0
Osprey (<i>Pandion haliaetus</i>)	E	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Broad-winged Hawk (<i>Buteo platypterus</i>)	E	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3
American Kestrel (<i>Falco sparverius</i>)	E	2.0 \pm 1.2	0.3 \pm 0.3	0.0 \pm 0.0	0.7 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0
Ruffed Grouse (<i>Bonasa umbellus</i>)	R	0.3 \pm 0.3	1.0 \pm 0.0	2.3 \pm 0.3	0.0 \pm 0.0	3.7 \pm 1.5	3.7 \pm 1.8
Greater Yellowlegs (<i>Tringa melanoleuca</i>)	L	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Solitary Sandpiper (<i>Tringa solitaria</i>)	L	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Common Snipe (<i>Gallinago gallinago</i>)	E	0.7 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.7 \pm 0.3	0.3 \pm 0.3	0.3 \pm 0.3
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	E	0.0 \pm 0.0	2.7 \pm 2.2	0.3 \pm 0.3	1.0 \pm 0.6	1.0 \pm 0.6	1.3 \pm 0.9
Downy Woodpecker (<i>Picoides pubescens</i>)	R	0.3 \pm 0.3	1.0 \pm 0.6	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0
Hairy Woodpecker (<i>Picoides villosus</i>)	R	3.0 \pm 1.0	1.3 \pm 0.9	0.0 \pm 0.0	0.7 \pm 0.3	0.3 \pm 0.3	0.7 \pm 0.7
Three-toed Woodpecker (<i>Picoides tridactylus</i>)	R	0.7 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Black-backed Woodpecker (<i>Picoides arcticus</i>)	R	2.3 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Northern Flicker (<i>Colaptes auratus</i>)	E	1.3 \pm 0.3	3.0 \pm 1.0	0.7 \pm 0.7	2.0 \pm 1.0	1.7 \pm 0.7	0.7 \pm 0.7
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	R	0.3 \pm 0.3	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	1.0 \pm 0.6	0.0 \pm 0.0
Western Wood-Pewee (<i>Contopus sordidulus</i>)	L	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0
Alder Flycatcher (<i>Empidonax alnorum</i>)	L	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	1.3 \pm 1.3	2.0 \pm 1.0	0.7 \pm 0.3
Least Flycatcher (<i>Empidonax minimus</i>)	L	0.0 \pm 0.0	0.0 \pm 0.0	1.7 \pm 1.2	0.3 \pm 0.3	1.0 \pm 0.0	0.0 \pm 0.0
Tree Swallow (<i>Tachycineta bicolor</i>)	E	0.7 \pm 0.7	4.3 \pm 2.0	1.3 \pm 0.3	1.7 \pm 0.9	0.0 \pm 0.0	0.0 \pm 0.0
Gray Jay (<i>Perisoreus canadensis</i>)	R	1.0 \pm 0.6	4.0 \pm 2.7	0.3 \pm 0.3	0.0 \pm 0.0	0.7 \pm 0.3	0.0 \pm 0.0
Blue Jay (<i>Cyanocitta cristata</i>)	E	0.0 \pm 0.0	0.0 \pm 0.0	0.7 \pm 0.3	0.0 \pm 0.0	1.0 \pm 0.6	1.0 \pm 1.0
Common Raven (<i>Corvus corax</i>)	R	1.0 \pm 0.6	0.0 \pm 0.0	1.3 \pm 0.9	0.0 \pm 0.0	0.3 \pm 0.3	1.7 \pm 0.3
Black-capped Chickadee (<i>Poecile atricapillus</i>)	R	1.3 \pm 0.3	2.0 \pm 1.2	6.0 \pm 1.5	0.7 \pm 0.3	7.0 \pm 1.0	3.3 \pm 0.9
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	R	0.3 \pm 0.3	1.0 \pm 0.6	1.7 \pm 0.9	1.3 \pm 0.7	1.3 \pm 0.9	2.0 \pm 1.2
Brown Creeper (<i>Certhia americana</i>)	E	2.3 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Winter Wren (<i>Troglodytes troglodytes</i>)	E	1.3 \pm 0.9	0.3 \pm 0.3	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Mountain Bluebird (<i>Sialia currucoides</i>)	E	0.3 \pm 0.3	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Swainson's Thrush (<i>Catharus ustulatus</i>)	L	0.0 \pm 0.0	1.0 \pm 0.6	1.7 \pm 0.7	0.0 \pm 0.0	1.0 \pm 0.6	1.7 \pm 0.7
Hermit Thrush (<i>Catharus guttatus</i>)	E	0.7 \pm 0.3	3.7 \pm 0.7	2.3 \pm 0.7	0.0 \pm 0.0	1.7 \pm 0.9	1.0 \pm 0.0
American Robin (<i>Turdus migratorius</i>)	E	1.0 \pm 0.0	3.7 \pm 1.9	1.7 \pm 0.3	0.7 \pm 0.7	0.0 \pm 0.0	1.0 \pm 0.6
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	L	0.0 \pm 0.0	1.7 \pm 1.7	0.0 \pm 0.0	1.0 \pm 0.6	0.3 \pm 0.3	0.7 \pm 0.7
Blue-headed Vireo (<i>Vireo solitarius</i>)	L	0.3 \pm 0.3	0.3 \pm 0.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3

APPENDIX. Continued.

Species	Migration category†	Number of years postfire			Number of years postharvest		
		1	14	28	1	14	28
Warbling Vireo (<i>Vireo gilvus</i>)	L	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.7 ± 0.3
Philadelphia Vireo (<i>Vireo philadelphicus</i>)	L	0.0 ± 0.0	1.0 ± 0.6	1.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.3	0.3 ± 0.3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	L	0.0 ± 0.0	5.7 ± 3.0	5.0 ± 1.2	0.3 ± 0.3	5.7 ± 0.3	5.7 ± 0.7
Tennessee Warbler (<i>Vermivora peregrina</i>)	L	0.0 ± 0.0	5.3 ± 0.9	19.0 ± 5.6	3.3 ± 1.5	15.3 ± 0.3	10.0 ± 0.6
Orange-crowned Warbler (<i>Vermivora celata</i>)	L	0.0 ± 0.0	1.3 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 1.0	0.0 ± 0.0
Connecticut Warbler (<i>Oporornis agilis</i>)	L	0.3 ± 0.3	0.0 ± 0.0	2.0 ± 1.0	0.0 ± 0.0	0.3 ± 0.3	0.3 ± 0.3
Yellow Warbler (<i>Dendroica petechia</i>)	L	0.0 ± 0.0	0.7 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	3.0 ± 1.5	0.7 ± 0.3
Magnolia Warbler (<i>Dendroica magnolia</i>)	L	0.0 ± 0.0	0.7 ± 0.7	0.7 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Cape May Warbler (<i>Dendroica tigrina</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	E	13.7 ± 11.2	0.3 ± 0.3	5.0 ± 3.5	1.0 ± 0.0	2.3 ± 0.7	1.7 ± 1.2
Black-and-white Warbler (<i>Mniotilta varia</i>)	L	0.0 ± 0.0	1.0 ± 0.6	2.3 ± 0.9	0.0 ± 0.0	3.7 ± 0.9	3.7 ± 1.2
American Redstart (<i>Setophaga ruticilla</i>)	L	0.0 ± 0.0	0.7 ± 0.7	0.7 ± 0.3	0.0 ± 0.0	8.0 ± 2.5	12.0 ± 2.0
Ovenbird (<i>Seiurus aurocapillus</i>)	L	0.0 ± 0.0	0.0 ± 0.0	9.3 ± 2.2	0.0 ± 0.0	1.3 ± 0.7	7.3 ± 2.2
Mourning Warbler (<i>Oporornis philadelphia</i>)	L	0.3 ± 0.3	1.0 ± 0.6	1.7 ± 0.3	6.0 ± 2.5	3.7 ± 1.8	3.7 ± 1.5
Common Yellowthroat (<i>Geothlypis trichas</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.7 ± 2.7	1.3 ± 0.9	0.3 ± 0.3
Canada Warbler (<i>Wilsonia canadensis</i>)	L	0.0 ± 0.0	0.3 ± 0.3	1.0 ± 1.0	0.0 ± 0.0	2.0 ± 1.2	5.3 ± 0.7
Western Tanager (<i>Piranga ludoviciana</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.7 ± 0.3
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	L	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.3	0.3 ± 0.3	4.3 ± 1.5	1.3 ± 0.3
Chipping Sparrow (<i>Spizella passerina</i>)	L	1.0 ± 1.0	0.0 ± 0.0	2.7 ± 1.2	2.7 ± 0.7	0.7 ± 0.3	1.0 ± 0.6
Clay-colored Sparrow (<i>Spizella pallida</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Le Conte's Sparrow (<i>Ammodramus leconteii</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.7 ± 2.7	0.0 ± 0.0	0.0 ± 0.0
Fox Sparrow (<i>Passerella iliaca</i>)	E	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
Song Sparrow (<i>Melospiza melodia</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	L	0.0 ± 0.0	2.7 ± 2.2	0.0 ± 0.0	11.7 ± 1.2	2.0 ± 0.6	0.3 ± 0.3
Swamp Sparrow (<i>Melospiza georgiana</i>)	L	0.0 ± 0.0	0.7 ± 0.7	0.7 ± 0.7	0.3 ± 0.3	0.7 ± 0.3	0.0 ± 0.0
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	L	10.7 ± 0.9	7.7 ± 0.3	14.7 ± 2.7	11.3 ± 2.3	12.3 ± 2.4	8.0 ± 2.1
Dark-eyed Junco (<i>Junco hyemalis</i>)	E	1.0 ± 0.6	0.7 ± 0.7	0.3 ± 0.3	3.0 ± 2.0	1.3 ± 0.7	1.3 ± 1.3
Rusty Blackbird (<i>Euphagus carolinus</i>)	E	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Brown-headed Cowbird (<i>Molothrus ater</i>)	E	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Purple Finch (<i>Carpodacus purpureus</i>)	L	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Pine Siskin (<i>Carduelis pinus</i>)	E	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.7 ± 0.7	1.0 ± 0.6	0.3 ± 0.3

† R, resident species, present in Alberta year round; E, early species, returning to the breeding grounds in Alberta before 1 May; L, late species, returning to the breeding grounds in Alberta after 1 May.