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POPULATION CHANGES IN BOREAL FOREST BIRDS IN SASKATCHEWAN AND MANITOBA

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ABSTRACT.—We counted breeding birds at four plots in central Saskatchewan and four in western Manitoba in 1990–1992 to examine changes in species composition and abundance since the plots were originally surveyed in 1972–1973. In Saskatchewan, more species of Neotropical migrants decreased (16) than increased (9; $P > 0.05 < 0.1$). Combined densities of Neotropical migrants declined (14–44%) on all of the Saskatchewan plots; Tennessee Warblers (*Vermivora peregrina*), Red-eyed Vireos (*Vireo olivaceus*), and Ovenbirds (*Seiurus aurocapillus*) declined on the most plots and by the greatest magnitude and Black-throated Green Warblers (*Dendroica virens*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) also decreased. Six of seven Neotropical migrants showed the same direction of change as in a province-wide Breeding Bird Survey. Successional changes did not account for decreased densities of these five species, but they may partly explain increases in some other species. Fluctuations in food supply (e.g., spruce budworm [*Choristoneura fumiferana*]) could not explain changes, because some species that should have responded numerically to budworm outbreaks that occurred in the 1990s had increased whereas others had decreased at the same site. The surrounding forest remained continuous over the 17–18 years, so changes in forest area cannot account for the declines. In Manitoba, more Neotropical migrants increased (19) than decreased (11) according to combined densities from four plots. Combined densities of Neotropical migrants also increased at three of the four plots (33–123%). Ten of 15 Neotropical migrant species showed different 'trends' than a province-wide analysis of BBS data. All changes in Manitoba could be attributed to vegetation succession on the plots and forest fragmentation in surrounding landscapes. Trends in Saskatchewan may be representative of general declines within continuously forested boreal landscapes, whereas those in Manitoba may reflect reduced opportunities for breeding in

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continuous forest as the landscape is increasingly fragmented by agriculture. *Received 3 Nov. 1995, accepted 22 May 1996.*

Widespread declines have been reported among forest birds that breed in North America and spend the boreal winter in the tropics (Neotropical-Nearctic migrants', hereafter 'Neotropical migrants'). Much of the evidence for these declines comes from long-term breeding bird censuses and Breeding Bird Surveys (BBS) in fragmented and isolated forests of the eastern and central United States (Johnston and Hagan 1992; for reviews see Askins et al. 1990; Askins 1993; Peterjohn and Sauer 1994). Deforestation and land-use change in the landscape surrounding the sites, and vegetation successional change on the plots themselves, are the likely causes of most local declines (Askins et al. 1990). That songbird populations have not decreased in some continuously forested areas (e.g., Wilcove 1988) supports the hypothesis that the small size and isolation of many eastern forests are crucial factors in the decline of some Neotropical migrants. However, songbird declines in other continuous forests (e.g., Holmes and Sherry 1988) and other factors provide increasing evidence to suggest that populations of some Neotropical migrants are also affected by events in the tropical nonbreeding areas because of competition for limited, and ever-diminishing, habitat (Marra et al. 1993; Rappole and McDonald 1994; Petit et al. 1995; Sherry and Holmes 1995; 1996).

Possible causes of declines in Neotropical migrants proposed for eastern North America include factors in the breeding areas, during migration, and in the nonbreeding areas (e.g., Holmes et al. 1986; Robbins et al. 1989; Askins et al. 1990; Hussell et al. 1992; Rappole and McDonald 1994; Sherry and Holmes 1995; 1996). In the boreal mixed-wood forest region of western Canada, which has a high diversity of breeding species and is the centre of distribution for some Neotropical migrants (e.g. Connecticut Warbler—scientific names are in Appendices I and II; Diamond 1991), it remains uncertain whether comparable declines have taken place. Moreover, the relative importance of the factors that affect songbird populations in western Canada may differ from those in the eastern or other parts of the continent. Boreal forest has been less subject to intensive human settlement than areas farther south where permanent fragmentation has resulted. Consequently, increases in populations of ground predators and the brood-parasitic Brown-headed Cowbird that accompany forest fragmentation elsewhere and which have been implicated in the decline of songbird populations (Robinson et al. 1995a) may be less important. Furthermore, the landscape changes that occur predominantly involve forestry operations; cutover areas do not change in their land-use and, indeed, may superficially resemble natural disturbances such as forest fire even though their effects on the forest landscape may be quite different (Hunter 1993; Telfer 1993). Some boreal species that appear 'area-sensitive' near the edges of their range in the United States may be less so within the boreal forest biome because this is a naturally heterogeneous habitat (Welsh 1987a; e.g., Merriam and Villard 1991). Therefore, long-term studies in continuous forest may be helpful to isolate the effects of factors other than forest size, cowbird parasitism, and possibly predation on bird populations.

We attempt to assess whether or not Neotropical migrants have declined in part of the boreal forest of western Canada by comparing densities in the early 1990s on eight Breeding Bird Census (BBC) plots in two locations counted by A. J. Erskine in the early 1970s, and comparing these changes at each site with those indicated by Breeding Bird Survey (BBS) data over the entire province (although largely south of continuous boreal forest in Saskatchewan and, to a lesser extent, Manitoba). Neither data set is ideal: the BBS routes have been run erratically (Erskine 1993) and, like the BBS routes elsewhere, they sample forest-interior species poorly because they are roadside counts. Also the BBC plots were counted in only two years about 20 years apart. We recognize these inherent flaws in design, but we believe it is important to present the data because there are no other sources of information than can address the question. Similar comparisons (of plots counted far apart in time), by Ambuel and Temple (1982) in southern Wisconsin and Wilcove (1988) in the Great Smoky Mountains, have set important precedents for making maximum use of opportunities to repeat early censuses despite problems in their inherent lack of replication.

METHODS

Study areas.—We counted birds on two study sites each containing four plots ranging from 15 to 30 ha in area. All plots, while within the Mixedwood zone of the Boreal forest, differed to some degree in vegetation and so there are some problems with treating them as replicates. Those in Saskatchewan were in a continuously forested area near Doré Lake (Erskine 1973a–d). Michel Point (17.5 ha, 54°41′N, 107°15′W) is a mature mixed stand of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*) with a few balsam poplar (*Populus balsamifera*). Except for the north end, the understory is generally sparse. Mirasty Lake (17.6 ha, 54°28′N, 107°14′W) is an even-aged stand dominated by trembling aspen with small numbers of white spruce, balsam fir (*Abies balsamea*), and black spruce (*Picea mariana*). A dense shrub layer of balsam fir occurs in the northern 150 m, and at the southern end speckled alder (*Alnus rugosa*), balsam poplar, and black spruce saplings are more abundant. Appleby Bay (17.5 ha, 54°29′N, 107°16′W) is an uneven-aged stand dominated by balsam fir with white birch, white spruce, trembling aspen, and some balsam poplar. Young balsam fir forms a dense shrub layer, and there are many mature blowdowns. A younger stand, dominated by white birch, trembling aspen, and white spruce occurs to the south. Doré Lake Airstrip (23.4 ha, 54°37′N, 107°23′W) is dominated by mature black spruce with little understory. Two small creeks within this site are bordered by willow (*Salix scouleriana*) and speckled alder.

The sites in western Manitoba, near Mafeking, were in a landscape increasingly influenced by agriculture but within the fringes of a large expanse of forest centred on the Porcupine Hills (Erskine 1972a–d). In 1972, Novra (17.5 ha, 52°31′N, 101°5′W) was a mature stand, undisturbed by human activity and dominated by balsam poplar and trembling aspen. The dense understory was composed mainly of mountain maple (*Acer spicatum*), beaked hazel (*Corylus cornuta*), and red osier (*Cornus stolonifera*). Speckled alder and willow (*Salix* spp.) occurred along three small brooks on the plot. By 1992, this stand had opened up considerably due to numerous blowdowns, creating more dense shrub in some locations and isolated large trees. The 1992 plot overlapped at least 95% with the 1972 plot; however, exact duplication of lines was not possible. Mafeking (17.5 ha, 52°47′N, 101°3′W) was a lowland black spruce stand; speckled alder and tamarack (*Larix laricina*) occurred in boggy gaps, and the main shrub was Labrador tea (*Ledum groenlandicum*). Around 1987, 30–40% of the 1972 plot was clear-cut, so in 1992 the plot was extended to the north in similar habitat to replace the cutover area. The northern 50% of the 1972 plot had changed little by 1992, except that trees were 1–2 m taller. Thus, this plot was 50% different and generally similar to that first surveyed in 1972, but lacking wet swales. Bellsite (29.25 ha, 52°35′N, 101°5′W) was dominated by jack pine (*Pinus banksiana*). Shrubs included Saskatoon serviceberry (*Amelanchier alnifolia*) and chokecherry (*Prunus virginiana*). Because the 1972 plot had been clear-cut and replanted with jack pine around 1987–1989 (30 cm height in 1992), an entirely new plot was established about 1.5 km farther north in roughly similar habitat but including small areas of planted pines. The Steeprock Bay plot (15.75 ha, 52°47′N, 100°55′W) was in a balsam fir and white birch stand with a few white spruces. The lower canopy was composed of white spruce and trembling aspen. According to Erskine (1972a–d), most large spruces were logged many years before. Where gaps occurred in the canopy, mountain maple, speckled alder (in wet areas), willow (*Salix discolor*), and beaked hazel grew. Changes since 1972 included clear-cutting of 10% of the 1972 plot and a further 10% cut-over for birch firewood. Thus, the 1992 plot was 10% smaller than the one censused in 1972. Also, windfalls of mature balsam fir had opened up the canopy.

Census techniques.—Territory mapping methods were used on all sites (Intl. Bird Census Comm. 1969; Bibby et al. 1992), and new 50-m grids for the 1990s censuses were placed as close as possible to the same lines used in the 1970s. In 1972 and 1973 all surveys were conducted by A. J. Erskine; PC censused the Saskatchewan plots in 1990 or 1991 and GEH censused the Manitoba plots in 1992. In Saskatchewan, plot coverage was from 27 May to 8 July in 1973 (8–10 visits per plot) and from 10 June to 28 June in 1990/1991 (9 visits per plot). Most counts in 1973 were between 04:05 and 12:46 h; in 1990 and 1991, most visits were between 04:13 and 11:40 h, with one evening visit (18:25–20:15 h). Less time was spent censusing each plot in 1973 because Erskine surveyed two plots each morning and all four plots (plus another wet-marshy bog census plot) in one year, whereas PC visited only one plot each morning and surveyed only two plots each year. The total counts from 1973 therefore are more likely underestimates compared with 1990–91. The weather in 1973 was generally cool with frequent rains (Erskine 1973a–d); in 1991 weather was similar, but in 1990 there was less cloud cover. In Manitoba, coverage was from 26 May to 7 July in 1972, and from 29 May to 24 June in 1992 (9 visits per plot for both periods). Counts were made between 04:55 and 13:22 h in 1972 and 04:30 to 12:45 h in 1992. Because GEH recorded more edge species and visitors, total counts for 1992 were higher than 1972 (A. J. Erskine pers. commun.). Erskine (1972a–d) recorded late May 1972 as being unusually warm. Frosts occurred on several days in mid-June 1972 (15, 19, 20), but censuses were generally on warm days.

Vegetation sampling.—Vegetation was quantified using the 0.04-ha (0.1-acre) circle sampling method of James and Shugart (1970). Five (1990/1991) or 20–28 circles (1972/1973) were placed at 50-m intersections of the bird census plot (these were located systematically in 1972/1973, randomly in 1990/1991). Diameters of all trees > 3 cm diameter at breast height (dbh) were measured in each circle, and canopy height was estimated visually. Shrub density was calculated as in James and Shugart (1970). Both canopy and ground cover were recorded on the second of the two transects used to estimate shrub density. Slight differences in class diameters for shrubs and trees used by PC in 1990–1991 caused us to combine some categories to provide data equivalent (but not fully comparable) to those collected by Erskine in 1973. The same protocol was used for measuring vegetation at the Manitoba sites in 1972, but different methods used in 1992 allowed us to calculate only the relative abundance of different tree species.

Interpretation of territories.—Because the interpretation of field data on breeding territories can differ between people (Oelke 1981; Bibby et al. 1992), original field sheets from all plots in both surveys were re-interpreted by DAK. This procedure avoided the bias of using interpretations by different individuals; we could not control for differences between the three field observers (A. J. Erskine and PC, and A. J. Erskine and GEH). Although we did not use the published data analyses of Erskine (1972 a–d, 1973 a–d), we compared the number of territories for each species and found that, with few exceptions, they were quite similar. For this analysis, it was the relative differences in densities between periods that were important.

We based territory boundaries on simultaneous registrations (contemporary contacts) by two singing males, because this gave the best indication that two different individuals held adjacent territories (Intl. Bird Census Comm. 1969). Territories were also determined by locating distinct clusters of song contacts recorded on different occasions (Intl. Bird Census Comm. 1969). We considered both the number of censuses and the spread of dates over which the censuses were made to recognize a cluster of registrations as delineating a territory. We considered 10 days between the first and last survey to be adequate following Marchant (1983).

In general, we used Intl. Bird Census Comm. (1969) criteria for the minimum number of registrations necessary for denoting breeding pairs; we considered two registrations (irrespective of the number of censuses) adequate for Black-capped Chickadee, Boreal Chickadee, Brown Creeper, Red-breasted Nuthatch, and woodpeckers, as these (mostly resident) species probably started breeding prior to the first census. Likewise, two registrations were considered sufficient for evidence of breeding by Cedar Waxwings because their breeding season extended later than the census period. The minimum period criterion between first and last censuses was also waived for this species. Finally, we counted all clusters within the plot and estimated the proportional area occupied at the edges of the plot to calculate total number of territories. Where species did not hold any full territories (partial clusters), we used a trace value (0.1) to represent possible breeders and visitors. However, we did not include these records in the main breeding totals for guild analyses for each plot because of uncertainties about their status. However, we included probable breeders (those with a + status in Erskine 1972a–d, 1973a–d). We excluded the four waterbirds, diurnal raptors, and large corvids from analyses because these species range over large areas and are not censused accurately by spot-mapping on plots of the sizes used. Flyovers of White-winged Crossbills, Pine Siskins, and Evening Grosbeaks were included, in both the 1970s and 1990s and territories of social groups (some of these species may nest semi-colonially) delineated to roughly estimate numbers of breeding pairs.

Analysis of life history strategies.—We classified species according to migratory habit and examined changes in combined densities of Neotropical migrants, short-distance migrants, residents, and irruptive species to test the possibility that the pattern of change between the two census periods might differ by life history strategy. Migratory strategy was assigned based on the literature and Canadian Wildlife Service databases (D. A. Welsh and J. Pedlar, unpubl. data, C. Downes, pers. commun.). Neotropical migrants were species mainly spending the boreal winter in Central and South America (south of 30°N latitude), short-distance migrants wintered mainly within Canada or the United States (north of 20° N latitude), and resident species were present throughout the year. We also distinguished irruptive species (i.e., Evening Grosbeak, White-winged Crossbill, Pine Siskin, and Purple Finch). However, in statistical analyses we combined irruptive species with residents because of small sample sizes.

Breeding Bird Survey (BBS) analyses.—to determine whether the patterns we observed at local census plots were part of a regional population change, we examined results from the BBS from 1973–1991 for Saskatchewan and 1972–1992 for Manitoba (B. T. Collins, pers. comm.). Standard route-regression techniques were used for BBS analyses with modifications described in Downes and Collins (1996).

Statistical analyses.—We calculated the combined densities of each species for Saskatchewan and Manitoba plots separately for each census period (1970s or 1990s). We believe this is justified because there was no replication of each habitat type. Then, using these totals, we tested whether Neotropical migrants, short-distance migrants, or resident (or irruptive) species declined overall using a Wilcoxon's Matched Pairs test (Zar 1984); here we used the 0.1 values because of small sample sizes (we omitted species that were recorded only as visitors at the edge of plots). We used chi-square one-sample tests (after Wilcove 1988) to compare the combined numbers of Neotropical migrants, short-distance migrants, and resident/irruptive species between years. Yates' correction was used because there was only one degree of freedom in all cases (Zar 1984). Chi-square tests were performed on actual number of territories and not the corrected density estimates (presented in Appendices I and II for comparison among plots). Except where stated, all statistical tests are two-tailed. It may be inappropriate to apply statistical tests to our data because our samples were not randomly chosen from wider populations and our sample sizes are small. We emphasize that our study design was constrained by the establishment of the plots in 1972 and 1973 and that our purpose is to explain possible trends; we recognize the impossibility of proving definite trends from eight plots counted 20 years apart.

RESULTS

Avifaunal changes: Saskatchewan.—Of 25 Neotropical migrant species counted at the four sites, 16 decreased and nine increased (Appendix I). Based on the null hypothesis that overall densities of Neotropical migrants should increase with succession in western boreal forests (see Kirk et al. 1996), as in eastern North America (Mönkkönen and Helle 1989), this decrease approached statistical significance ($T = 105.5$, $N = 25$, one-tailed probability, $0.1 > P > 0.05$). However, there were marked decreases in five Neotropical migrant species; Red-eyed Vireos declined by 48% at Michel Point, where they were most abundant, and at two other sites (Mirasty Lake 65%, Appleby Bay 91%; Appendix I). At another site (Doré Lake) they occurred at low abundance in 1973 and disappeared

TABLE 1

CHANGES IN HABITAT VARIABLES IN SASKATCHEWAN AND MANITOBA CENSUS PLOTS

Site	Year	Ground cover (%)	Shrub density[a] (stems/ha)	Canopy cover (%)	Canopy height $\bar{x}$	Canopy height Range
Saskatchewan						
Michel Point	1973	82	1750	80	18.9	15.0–21.6
	1990	78	5625	74	23.5	20.5–26.4
Mirasty Lake	1973	63	2875 (5525)	71	10.2	6–12
	1991	76	6700	81	16.7	14.4–18.9
Appleby Bay	1973	54	2050 (4610)	72	16.2	9–24
	1991	57	6850	80	19.6	17.4–21.6
Doré Lake	1973	80	1738 (3350)	53	12.9	
	1990	90	6525	53	17.7	10.8–27.3
Manitoba						
Novra	1972	<50	23,000	75	17.1	9.0–21.0
	1992					
Mafeking	1972	98	2623	55	10.8	9.0–13.5
	1992					
Bellsite	1972	95	1255	42	8.1	6.0–12.0
	1992					
Steeprock Bay	1972	95	4143	64	12.6	9.0–16.5
	1992					

[a] Note that in 1972/1973 Erskine measured trees in 3.75–7.5 cm and >7.5 cm classes (in parenthesis), plus shrubs separately. PC measured shrubs <7.5 cm; thus Erskine's combined trees <7.5 cm and shrub classes should be equivalent to PC's estimates. However, other differences interfered with comparisons.

completely by 1990. Tennessee Warblers declined at all sites; by 98% at Michel Point, 69% at Mirasty Lake, 27% at Appleby Bay, and 39% at Doré Lake. Black-throated Green Warblers also declined at Michel Point (76%) and at Appleby Bay (67%). Ovenbirds declined (46%) at Michel Point and (29%) at Mirasty Lake. Rose-breasted Grosbeaks declined 92% at Michel Point and 83% at Appleby Bay (Appendix I).

In contrast to Neotropical migrants, there were no consistent patterns of declines across sites in 13 short-distance migrant species. Seven species declined, six increased, and in one there was no change ($T = 34.5$, $N = 13$, $P > 0.1$; Appendix I). However, there was a difference ($T = 3$, $N = 11$, $P < 0.02$) in the magnitude of the increases (9) and decreases (2) in irruptive and year-round resident species. This may be because of the widely fluctuating nature of local populations of nomadic species, depending on food supply.

Migratory status.—There were striking differences between the two count periods when we compared the overall number of individuals by migratory strategies (Fig. 1). The combined densities of Neotropical migrants declined on all four plots (Fig. 1). Combined densities of Neotropical migrants declined 44% at Michel Point ($\chi^2 = 11.36$, df 1, $P < 0.001$), 40% at Mirasty Lake ($\chi^2 = 3.52$, df 1, $P > 0.05$) and 25% at Appleby Bay ($\chi^2 = 1.78$, df 1, $P > 0.1$). The non-significant decrease ($\chi^2 = 0.17$, df 1, $P > 0.5$) in numbers of Neotropical migrants at Doré Lake was much smaller (14%; Fig. 1). However, short-distance migrant species increased on all plots, although the densities were much lower; 184% at Michel Point ($\chi^2 = 1.76$, df 1, $P > 0.1$), 135% at Mirasty Lake ($\chi^2 = 0.17$, df 1, $P > 0.5$), and 37% at Doré Lake ($\chi^2 = 1.19$, df 1, $P > 0.1$). There was little change in the combined densities of this group (10% increase) at Appleby Bay ($\chi^2 = 0$, df 1, $\mathrm{P} > 0.9$). Similarly, combined densities of resident and irruptive species increased at three sites, although the difference was significant only for Doré Lake (176%, $\chi^2 = 5.98$, df 1, $P < 0.025$; Fig. 1). There was a slight decrease at Appleby Bay (5%).

Vegetation changes.—The vegetation at Michel Point had become slightly more uneven-aged over the period between censuses, with an increase in the proportion of larger trees (Fig. 2). Opening of the lower canopy may have occurred through windfall. There was an increase in relative density of white spruce, balsam fir (> 3 cm dbh), and aspen, but balsam poplar densities declined in 1991 (Fig. 3), possibly due to blowdowns. However, these differences could be attributed to sampling variation. Mirasty Lake was a successional aspen stand following a fire 30 years prior to the first census. This area had an increase in relative densities of white spruce and balsam fir (> 3 cm dbh; Fig. 3) and in canopy cover. Balsam fir dominated at Appleby Bay in both periods but there was a small increase in the proportion of aspen and a larger increase in white birch (Fig. 3). The increase in the proportion of shade-intolerant hardwood trees (Fig. 3) was accompanied by an increase in canopy cover (Table 1). The site that changed least in vegetation characteristics was Doré Lake Airstrip (Figs. 2, 3). However, there was a slight increase in relative density of black spruce, and more deciduous tree species were recorded in 1991 than 1973. The apparent increase in shrub densities at all sites (Table 1) may be unreliable because of differing sample sizes and methods; the relative values within years may, however, be useful.

Avifaunal changes: Manitoba.—There were no consistent patterns of declines or increases in Neotropical migrants over the 20-year period at the four sites in the Mafeking region (Appendix II). More species increased (19) than decreased (11), and the difference between years was not significantly different ($T = 139$, $\mathrm{N} = 30$, $P > 0.1$). Of the species that decreased, the Solitary Vireo was most notable (by 89% at Steeprock Bay, 86% at Bellsite and 18% at Mafeking). Other species such as Tennessee Warbler disappeared at Bellsite and Mafeking but stayed the same

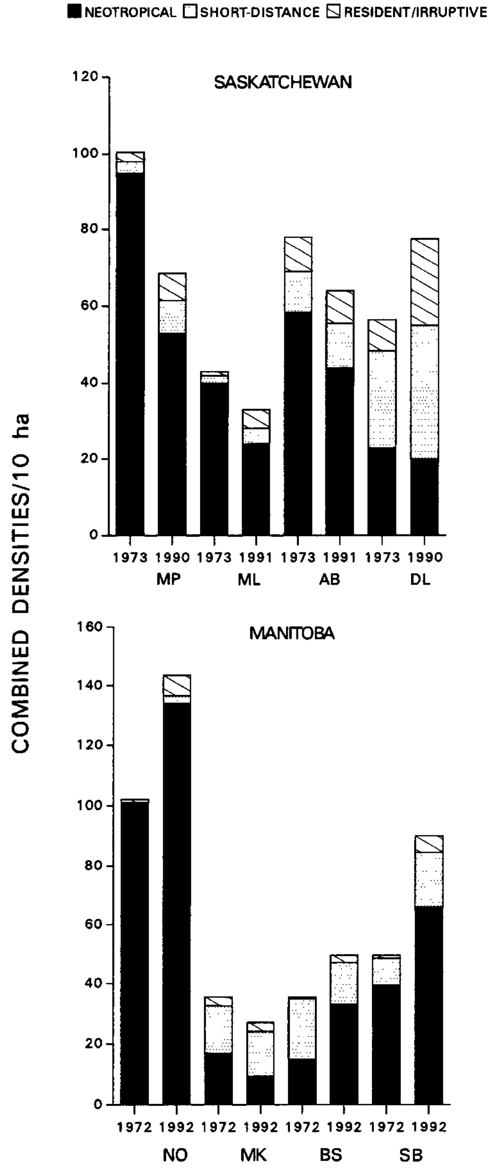


FIG. 1. Combined densities of Neotropical migrants, short-distance migrants, and residents/irruptive species. MP = Michel Point, ML = Mirasty Lake, AB = Appleby Bay, DL = Doré Lake; NO = Novra, MK = Mafeking, BS = Bellsite, SB = Steeprock Bay.

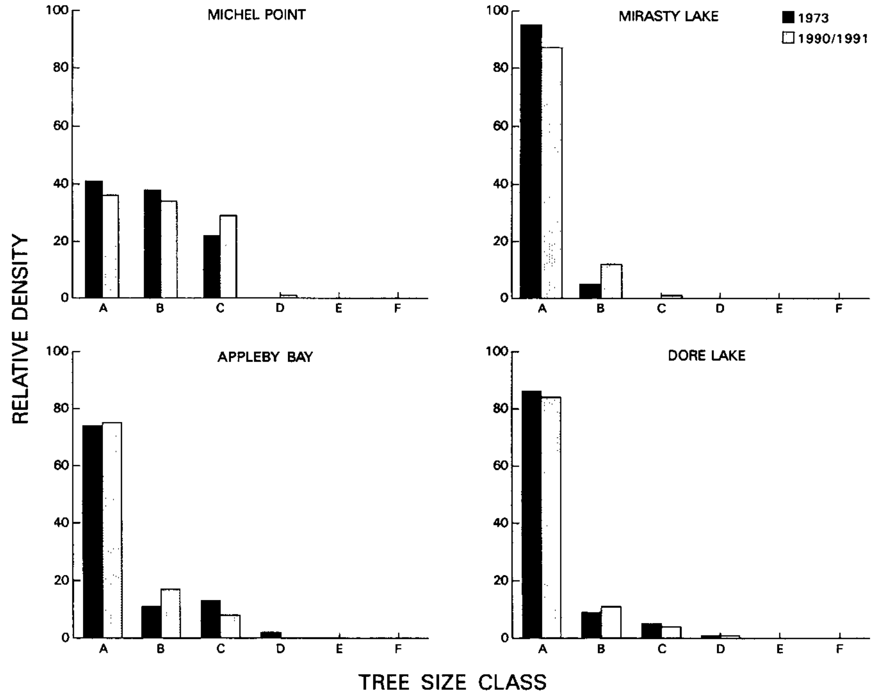


FIG. 2. Changes in proportions of tree size classes at Michel Point, Mirasty Lake, Appleby Bay, and Doré Lake Airstrip (size classes: A = 7.5–15 cm, B = 17.5–22.5, C = 32.5–37.5, D = 40.0–52.5, E = 55.0–67.5, F = 70.0–82.5). Erskine (1973) also considered trees of 3.5–7.5 cm diameter but these are excluded from analysis here.

(at Novra) or increased (at Steeprock Bay). Both of these species occurred at relatively low densities. The magnitude of change in the species that increased was far greater: at Novra, Least Flycatcher increased (200%) as did Swainson's Thrushes (248%), Red-eyed Vireos (100%) and Canada Warblers (406%). At Steeprock Bay, increases were found for Magnolia Warbler (32%) and Ovenbird (340%). Of the short-distance migrants, eight increased and nine decreased ($T = 54.5$, $N = 17$, $P > 0.1$; Appendix I). There was a significant increase in abundance of residents and irruptive species ($T = 16.5$, $N = 15$, $P < 0.02$), with 12 increasing and only three decreasing.

Migratory status.—Combined densities of Neotropical migrants increased significantly at three plots in Manitoba; 33% at Novra ($\chi^2 = 4.36$, df 1, $P < 0.05$), 67% at Steeprock Bay ($\chi^2 = 6.16$, df 1, $P < 0.025$), and 125% at Bellsite ($\chi^2 = 6.02$, df 1, $P < 0.025$; Fig. 1). The only site where this group declined (41%) was at Mafeking ($\chi^2 = 1.59$, df 1, $P > 0.1$).

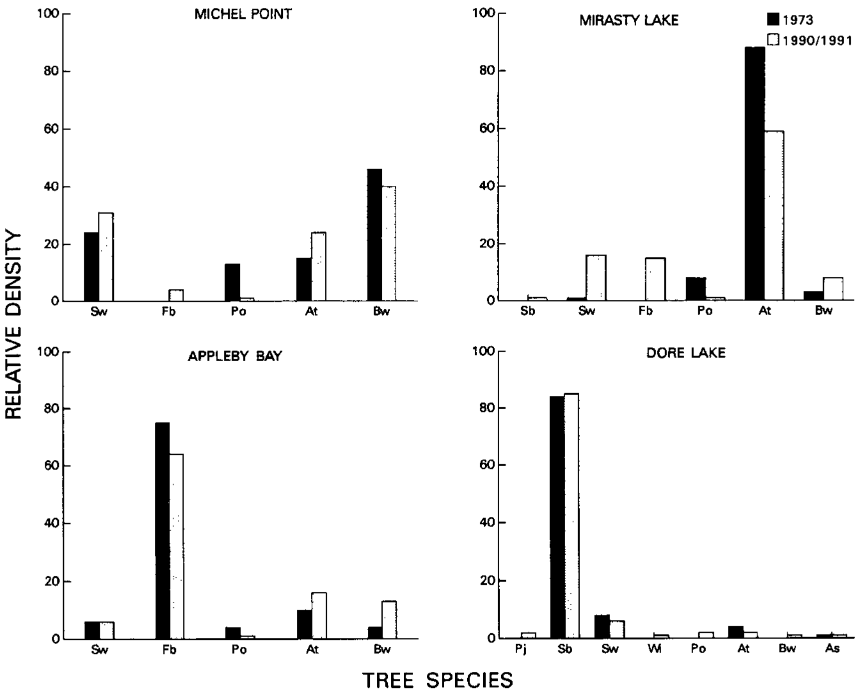


FIG. 3. Changes in proportions of tree species at Michel Point, Mirasty Lake, Appleby Bay, and Doré Lake Airstrip (tree species: Pj = jack pine, Sb = black spruce, Sw = white spruce, Fb = balsam fir, Wi = scouler willow, Po = balsam poplar, At = trembling aspen, Bw = white birch, As = speckled alder)

Short-distance migrants increased non-significantly at Steeprock Bay (106%, $\chi^2 = 2.63$, df 1, $P > 0.1$); low densities at Novra prohibited statistical testing. There were non-significant decreases in this group at Mafeking and Bellsite ($\chi^2 = 0$, df 1, $P > 0.9$ and $\chi^2 = 0.74$, df 1, $P > 0.5$, respectively). Resident and irruptive species increased at all sites, but none of the increases were significant and actual densities were very low (Fig. 1).

Vegetation changes.—The plot that differed most in its vegetation structure over the 20-year period was Novra. This balsam poplar site was mature at the time of the first census. By 1992, this stand had become open because of aging and windthrow; hence the decline in relative densities of poplar, aspen, and birch (Fig. 4). Consequently, there were more open areas and probably increased shrub density at this site, as well as isolation of mature trees. At Steeprock Bay, increased shrub densities were a result of a more open canopy cover due to logging and windthrow.

TABLE 2

BREEDING BIRD SURVEY RESULTS FOR SASKATCHEWAN AND MANITOBA (B. T. COLLINS, PERS. COMMUN.)

	Saskatchewan 1973–1991				Manitoba 1972–1992			
			Mean abundance				Mean abundance	
Species	% change	N	73	90/91	% change	N	72	92
Long-distance migrants								
Least Flycatcher	3.4**[a]	42	2.6	4.6	−3.2	34	8.8	4.6
Great Crested Flycatcher	—	—	—	—	1.6	26	0.8	1.0
Veery	—	—	—	—	1.9	24	0.6	0.9
Swainson's Thrush	−5.8	11	2.7	0.9	−2.2	15	3.8	2.4
Red-eyed Vireo	0.4	33	3.6	3.9	−0.7	32	6.8	5.9
Tennessee Warbler	−3.0	12	1.2	0.7	1.1	20	1.1	1.4
Nashville Warbler	—	—	—	—	−7.0	14	8.8	2.1
Yellow Warbler	1.5**	43	4.1	5.4	—	—	—	—
Chestnut-sided Warbler	—	—	—	—	2.5	15	1.5	2.4
American Redstart	—	—	—	—	−7.4	18	0.6	1.2
Ovenbird	−7.6	13	3.6	0.9	2.2	18	3.1	4.7
Connecticut Warbler	—	—	—	—	−7.6	15	2.5	0.5
Mourning Warbler	—	—	—	—	−2.2	19	3.6	2.3
Common Yellowthroat	—	—	—	—	−2.4	33	7.6	4.6
Rose-breasted Grosbeak	−0.1	18	0.9	0.9	−4.9	29	2.1	0.9
Clay-colored Sparrow	—	—	—	—	−2.9	33	21.2	11.7
Short-distance migrants								
Ruby-crowned Kinglet	—	—	—	—	0.9	13	1.5	1.7
Hermit Thrush	6.5**	12	0.6	1.9	1.1	14	2.1	2.6
Cedar Waxwing	—	—	—	—	−6.5	30	5.9	1.5
Yellow-rumped Warbler	—	—	—	—	5.1	17	0.9	2.5
Chipping Sparrow	−10.6	37	4.6	0.6	−0.9	34	4.3	3.6
Vesper Sparrow	—	—	—	—	0.9	30	5.9	7.0
Song Sparrow	—	—	—	—	−1.8	34	13.9	9.7
White-throated Sparrow	2.3	13	2.1	3.1	−1.6	19	7.4	5.4
Dark-eyed Junco	−1.5	10	0.8	0.6	—	—	—	—
Irruptive species								
Pine Siskin	1.0	13	0.5	0.6	—	—	—	—
Purple Finch	—	—	—	—	6.2	14	4.7	0.2
Year-round residents								
Ruffed Grouse	−1.6	17	0.5	0.4	—	—	—	—
Downy Woodpecker	—	—	—	—	1.5	26	0.4	0.5
Hairy Woodpecker	—	—	—	—	−0.9	29	0.7	0.6
Pileated Woodpecker	—	—	—	—	4.1	16	0.3	0.7
Gray Jay	—	—	—	—	−0.9	11	2.3	2.0
Black-capped Chickadee	−0.5	25	0.8	0.7	—	—	—	—
White-breasted Nuthatch	—	—	—	—	−14.8	15	0.2	0.7

[a] Significance levels are * $0.05 < P < 0.1$; ** $P < 0.05$). Species with abundance values of ≤ 0.2/10 ha for 1970s or 1990s in Appendices I and II are excluded.

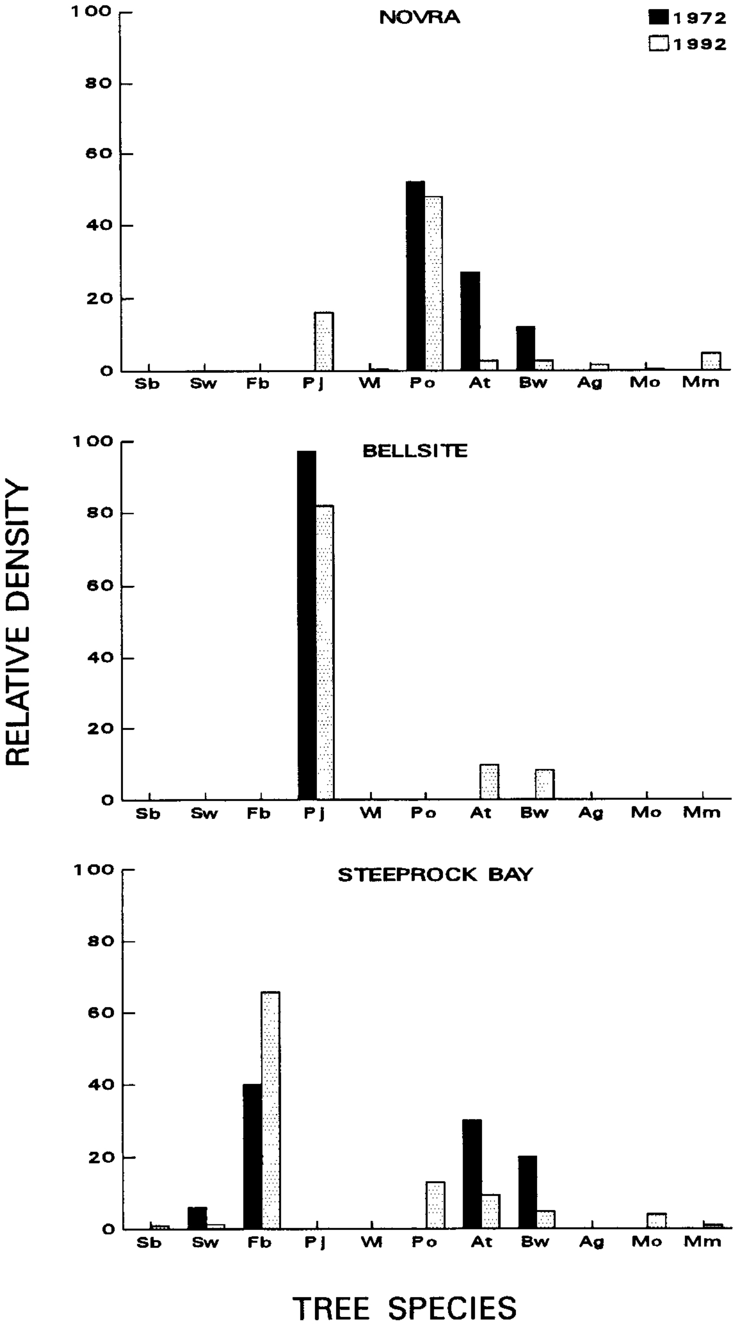
It is not surprising that few vegetation changes occurred at the Mafeking site because it was dominated by black spruce and succession in such stands is slow. At Bellsite, the jack pine plot was more mixed than that surveyed in 1972; the deciduous component was greater (Fig. 4) and pines were of larger size.

Breeding Bird Survey results.—We compared our data with analyses from the Breeding Bird Survey for the periods 1973–91 and 1972–92 for each province, respectively, to see if similar trends were reported at the scale of entire provinces (B. T. Collins, pers. commun.). The same direction of regression coefficients was found in the BBS as in the changes at our study sites in Saskatchewan for six of the seven Neotropical migrants reported on 10 or more routes (compare Appendices I and II vs Table 2). For example, there was a significant increase in Least Flycatchers and Yellow Warblers according to the BBS. Most strikingly, two of the species that showed the greatest declines in our study (Tennessee Warbler and Ovenbird) had negative regression coefficients according to the BBS for Saskatchewan (Table 2). However, Red-eyed Vireos had a positive regression coefficient (Table 2). In contrast to the results for Saskatchewan, the direction of BBS regression coefficients for Neotropical migrants in Manitoba were often opposite to the results we found (10 out of 15 cases; Table 2). For example, while Least Flycatchers decreased significantly in Manitoba over the long-term, they increased at one of our sites and began breeding at two others. However, unless the slope in route-regression analyses are significant, the direction of BBS regression coefficients may not be meaningful, so we urge caution in the interpretation of these comparisons.

DISCUSSION

We acknowledge the limitations of our data, which compare only two points in time two decades apart; we recognize that populations may have fluctuated considerably in the intervening years (e.g., Holmes and Sherry 1988; Blake et al. 1994). We do not know how representative our plots may be of boreal mixed-wood forests in the region in general, and we acknowledge that changes apparent on small plots may be stabilized at larger geographic scales (the metapopulation level; Villard et al. 1992). Nevertheless, our data are the first long-term plot-based 'trends' to be reported from an important area of the boreal forest, and they illustrate some problems of more general interest.

Although Neotropical migrants as a group did not decline significantly in Saskatchewan, five species declined on all plots where they were censused over the 17-year period, and combined densities of Neotropical migrants decreased on all sites. In contrast, Neotropical migrant numbers


NOVRA
■ 1972
□ 1992
BELLSITE
STEEPROCK BAY
RELATIVE DENSITY
0
20
40
60
80
100
Sb
Sw
Fb
Pj
Wl
Po
At
Bw
Ag
Mo
Mm
TREE SPECIES

tended to increase or remain stable in Manitoba. The Saskatchewan results recall those from fragmented forests in the eastern U.S., rather than those reported by Wilcove (1988) in the extensive forests of the Great Smoky Mountains; yet our Saskatchewan plots were in contiguous, unfragmented forest. The changes in bird abundance in Saskatchewan also run counter to predictions that Neotropical migrant numbers should increase as the forest matures (Mönkonen and Helle 1989) as found at other sites in western Canada (Kirk et al. 1996).

Regional differences in population trends of Neotropical migrants have been described elsewhere (James et al. 1992; Sauer and Droege 1992). We believe that the differences we found between the provinces are partly attributable to forest succession and the more fragmented nature of the landscape of the Manitoba plots. These were already somewhat fragmented by human settlement in 1972, and much forest has since been cleared for agriculture, mainly on the Swan Lake plain but also by the highway close to Mafeking. Logging has also become more widespread since a pulp mill was opened at La Pas in the mid 1980s, and a new mill is about to open in the Mafeking area (P. Rakowski, pers. commun.). The Manitoba plots, although still in forest, are now adjacent to an increasingly agricultural landscape; the Saskatchewan plots, in contrast, remain in a predominantly unfragmented forested landscape. The Manitoba study area is close to continuous forest in the Porcupine Hills which has high populations of Neotropical migrants (A. R. Smith pers. obs.). Thus, this census area may function as a population sink (sensu Pulliam and Danielson 1991; Villard et al. 1992). High apparent densities of Neotropical migrants have been found in fragmented boreal forest elsewhere in Saskatchewan (K.A. Hobson, pers. commun.) and in isolated, fragmented forests in the United States (Robinson et al. 1995a; Brawn and Robinson 1996).

In a comparison of bird populations trends between 1969–1986 at local (Hubbard Brook Experimental Station, New Hampshire) and regional scales (BBS statewide trends), Holmes and Sherry (1988) found that 10 of 19 bird species followed the same direction of trends. More species showed significant declines than increases at both the local (8 vs 1) and regional scale (5 vs 1). However, only three Neotropical migrant species decreased significantly at both scales (Least Flycatcher, Swainson's

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←

FIG. 4. Relative densities of different tree species at (a) Novra, (b) Bellsite and (c) Steeprock Bay (Sb = black spruce, Sw = white spruce, Fb = Balsam fir, Pj = jack pine, Wi = willow species, Po = balsam poplar, At = trembling aspen, Bw = white birch, Ag = speckled alder, Mo = mountain maple, Mm = Manitoba maple).

Thrush, and Wood Thrush). Our analysis of BBS results over the same periods as encompassed by our study supports our finding that Tennessee Warblers and Ovenbirds may have declined in Saskatchewan boreal forest. Banding data since the 1950s also suggest that Tennessee Warblers may be declining in Saskatchewan (Smith and Diamond 1993), although trends in this species are difficult to determine because it is a budworm specialist. These results suggest that the declines we observed in Saskatchewan may not be limited to our plots but may be part of larger-scale phenomena. The BBS data are not conclusive either, because the regression coefficients were not statistically significant and may reflect cyclic population fluctuations (Hussell et al. 1992); densities of Tennessee Warblers fluctuated dramatically (Welsh 1987b) and were 'puzzlingly high' on the Saskatchewan plots in 1973 (A. J. Erskine, pers. commun.). Ovenbird populations may also fluctuate greatly from year to year in fragmented habitats (Gibbs and Faaborg 1990).

Because the Saskatchewan sites were not logged or the surrounding forest fragmented in the 17 years between counts, what might have caused the declines in the five species of Neotropical migrants? In a 16-year study of bird populations on a 10 ha plot at the Hubbard Brook Experimental Station, New Hampshire, Holmes et al. (1986) identified five factors that affected songbird population densities; (1) food supply (especially defoliating Lepidoptera); (2) poor spring weather conditions; (3) forest successional changes; (4) competitive interactions and (5) nonbreeding mortality. We will address each of these in turn.

At Hubbard Brook, Lepidopteran outbreaks accounted for high densities of Scarlet Tanager (*Piranga olivacea*), Least Flycatcher, Red-eyed and Philadelphia vireos and most warbler species during the first three years of study; long-term declines were attributed to lows in Lepidopteran populations which fluctuate on a 6–10 year irregular basis (Holmes et al. 1986). Evidence for changes in food supply causing bird density changes in our study area was weak; unfortunately, we had little information on the timing of Lepidopteran outbreaks. Although spruce budworm (*Choristoneura fumiferana*) outbreaks struck Mirasty Lake and Appleby Bay in 1990 and 1991, among budworm specialists only Bay-breasted Warblers showed numerical increases, while Cape May Warblers were new breeders at Appleby bay in 1991. Contrary to expectations, Tennessee Warblers declined dramatically at both sites; declines in other warbler species that should also respond numerically to budworm irruptions (Hussell et al. 1992) argue against the food supply hypothesis for the Saskatchewan sites. So far as we know the only other Lepidopteran outbreak was of tent caterpillars (*Malacosoma disstria*) which defoliated aspens near Michel Point in 1973. Subsequent movement by Red-eyed Vireos seeking alternative foraging habitat in the birch on that plot could explain the high densities in 1973.

Cold, wet weather in late May (1974) was linked to declines in Scarlet Tanagers and several other species at Hubbard Brook (Holmes et al. 1986). While rain occurred on most survey days in 1973 in this study (A. J. Erskine, pers. commun.), the weather was dry in 1990 or 1991. Had weather influenced counts, bird numbers should have increased between censuses, not decreased.

Changes in habitat suitability possibly accounted for the decline of Least Flycatchers, Philadelphia Vireos, and Wood Thrushes at Hubbard Brook (Holmes et al. 1986). Our 1990s vegetation surveys were not strictly comparable with those of 1973; they do not show the requisite changes in forest structure that could have caused declines in the five species in Saskatchewan, but the differences in bird numbers recorded in Manitoba were consistent with succession.

Interspecific aggression by Least Flycatchers affected habitat use by American Redstarts at Hubbard Brook. We have no data on interspecific competition, but the bird communities were similar in the two study areas, so this factor is unlikely to have been important.

Finally, evidence for winter limitation on breeding numbers at Hubbard Brook was found for Dark-eyed Junco and Hermit Thrush, both of which declined after cold winters in the United States; little evidence was found to suggest that Neotropical migrants were affected by events during the nonbreeding season. While the effect of tropical habitat change is controversial (Hutto 1988, Robbins et al. 1989, Askins et al. 1990, Hussell et al. 1992), it is now recognized that nonbreeding survival rates for many species depend on the availability of suitable forest habitat in the Neotropics, which is declining rapidly.

Except for the Red-eyed Vireo, which spends the boreal winter in South America, there is considerable overlap in the nonbreeding distribution of Tennessee Warbler, Black-throated Green Warbler, Ovenbird, and Rose-breasted Grosbeak (Rappole et al. 1995), all species that declined at the Saskatchewan plots. The main difference is that Tennessee Warblers do not 'winter' in the Caribbean, while Black-throated Green Warblers and Ovenbirds do. Also the range of Rose-breasted Grosbeaks extends farther into South America than those of the warblers, occurring in much of Venezuela and Colombia, as well as Ecuador and Peru (Rappole et al. 1995). Most nonbreeding habitat for Red-eyed Vireos is in the Amazon Basin (Brazil), while for Tennessee Warblers, Black-throated Green Warblers, and Ovenbirds it is in western or southern Mexico. Most nonbreeding habitat for Rose-breasted Grosbeaks is in Colombia and Panama and, to a lesser extent, Mexico (Diamond 1986). Thus, the possibility exists that where the nonbreeding areas of some Saskatchewan subpopulations of these species overlap, they are all being affected by loss of preferred habitat. Both Black-throated Green Warbler and Ovenbird were included by Petit et al. (1995) in a list of 45 species vulnerable to destruction of tropical broadleaved forests.

Recent studies suggest that the species that declined at the Saskatchewan plots use a range of forest habitats in the Neotropics (Hutto 1992; Greenberg 1992; Wunderle and Waide 1993; see review by Petit et al. 1995). In the Caribbean, Yucatan Peninsula, and western Mexico, Black-throated Green Warblers and Ovenbirds occur at highest densities in forest (Hutto 1992; Greenberg 1992; Wunderle and Waide 1993) and are considered forest generalists (Lynch 1989; Greenberg et al. 1995). Red-eyed Vireos are most abundant in early to mid-successional or edge habitats and are relatively rare in primary forests in the Amazon lowlands and adjacent Andes (S. K. Robinson, pers. commun.; Robinson et al. 1995b). Tennessee Warblers prefer patches of remnant forest and open woodland (e.g. Costa Rica; Powell et al. 1992), and Rose-breasted Grosbeaks use field-forest vegetation in western Mexico and the Yucatan (Lynch 1989; Hutto 1992). However, evaluating habitat for Neotropical migrants based on the distinction between forest and non-forest habitats may be a false dichotomy. While none of the above species uses completely open agricultural field habitats, they do use forest patches, gallery strips, or hedgerows within human-altered landscapes. As has been pointed out by others (Lynch 1989; Greenberg 1992; Petit et al. 1995), decreased habitat suitability may not just involve loss of mature forest; in much of the Neotropics second growth and forest habitat patches are also disappearing rapidly. Also, habitat use of Neotropical migrants is usually assessed from point counts or mist-net surveys in small areas, without measures of survival or differing social systems. That more individuals of Neotropical migrants are counted in early successional or patchy habitats, therefore, does not contradict the hypothesis that populations could be partly limited during the boreal winter (see Rappole and McDonald 1994). For example, Tennessee Warblers occur at highest densities in coffee plantations in parts of Mexico (Greenberg et al. 1995; in press). The shift from shade coffee to sun coffee in recent years in parts of the Neotropics may have become a limiting factor for this species because of loss of flowering tree species important for foraging (R. Greenberg pers. commun.).

However, since the same species that declined in Saskatchewan did not do so in Manitoba, and considerable mixing of populations is likely in the Neotropics (Wilcove and Terborgh 1984), it seems hard to attribute the trends we found to effects in the nonbreeding areas. It is possible, however, that the Manitoba densities were raised by successional and fragmentation influences sufficiently to mask or reverse an underlying downward trend reflected in the contiguous forests of Saskatchewan.

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APPENDIX I

ESTIMATED NUMBER OF PAIRS/10 HA AT DORÉ LAKE, SASKATCHEWAN CENSUS SITES

	Michel Point		Mirasty Lake		Appleby Bay		Doré Lake		Total	
Common and scientific name	1973	1990	1973	1991	1973	1991	1973	1990	1973	1990–91
Long-distance migrants										
Olive-sided Flycatcher (*Contopus borealis*)							0.1		0.1	0
Yellow-bellied Flycatcher (*Empidonax flaviventris*)			0.1	0.9	0.1			0.1	0.2	1.0
Alder Flycatcher (*E. alnorum*)							0.1		0.1	—
Least Flycatcher (*E. minimus*)	4.6	6.9							4.6	6.9
Swainson's Thrush (*Catharus ustulatus*)		0.6	1.7	2.3	6.3	4.0	0.9	0.9	8.9	7.8
Solitary Vireo (*Vireo solitarius*)						1.7		0.9	0	2.6
Philadelphia Vireo (*V. philadelphicus*)			0.6	0.1					0.6	0.1
Red-eyed Vireo (*V. olivaceus*)	15.4	8.0	3.1	1.1	1.1	0.1	0.1		19.7	9.2
Tennessee Warbler (*Vermivora peregrina*)	8.0	0.2	7.4	2.3	6.3	4.6	5.6	3.4	27.3	10.5
Yellow Warbler (*Dendroica petechia*)		1.7							0	1.7
Magnolia Warbler (*D. magnolia*)		1.1	0.3		5.7	0.1		0.1	6.0	1.3
Cape May Warbler (*D. tigrina*)						1.1	1.7	0.9	1.7	2.0
Black-throated Green Warbler (*D. virens*)	4.6	1.1			4.3	1.4			8.9	2.5
Blackburnian Warbler (*D. fusca*)	0.1	0.2							0.1	0.2
Palm Warbler (*D. palmarum*)				0.1					0	0.1
Bay-breasted Warbler (*D. castanea*)	2.3	0.1		0.9	6.3	9.1	0.4	0.4	9.0	10.5
Black-and-white Warbler (*Mniotilta varia*)			1.1	0.1					1.1	0.1
American Redstart (*Setophaga ruticilla*)			0.1						0.1	0
Ovenbird (*Seiurus aurocapillus*)	16.0	8.6	8.0	5.7		0.1$^+$			24.0	14.4
Mourning Warbler (*Oporornis philadelphia*)	0.1								0.1	0
Canada Warbler (*Wilsonia canadensis*)			0.1		0.3				0.4	0
Western Tanager (*Piranga ludoviciana*)		1.1							0	1.1
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1.2	0.1			0.6	0.1			1.8	0.2
Chipping Sparrow (*Spizella passerina*)	2.3	0.6	0.6	0.6	2.3	2.9	1.5	1.7	6.7	5.8
Lincoln's Sparrow (*Melospiza lincolnii*)							0.1		0.1	0
Short-distance migrants										
Yellow-bellied Sapsucker (*Sphyrapicus varius*)					0.1				0.1	0
Northern Flicker (*Colaptes auratus*)							0.1		0.1	0
Blue Jay (*Cyanocitta cristata*)					0.1				0.1	—
Red-breasted Nuthatch (*Sitta canadensis*)		0.1$^+$		0.1$^+$	0.1$^+$	1.1		0.4	0	1.7
Brown Creeper (*Certhia americana*)		0.6				0.6	0.2	2.1	0.2	3.3
Winter Wren (*Troglodytes troglodytes*)					2.9	2.6	0.1$^+$	0.1$^+$	3.0	2.7

APPENDIX I
CONTINUED

Common and scientific name	Michel Point		Mirasty Lake		Appleby Bay		Doré Lake		Total	
	1973	1990	1973	1991	1973	1991	1973	1990	1973	1990–91
Golden-crowned Kinglet (*Regulus satrapa*)						0.1	0.9	0.9	0.9	1.0
Ruby-crowned Kinglet (*R. calendula*)		0.1		0.1	0.1		2.6	4.7	2.7	4.9
Hermit Thrush (*Catharus guttatus*)		0.1	1.1	0.1					1.1	0.2
Cedar Waxwing (*Bombycilla cedrorum*)								0.1^+	0	0.1
Yellow-rumped Warbler (*Dendroica coronata*)	1.7	2.9		2.3	1.2	2.3	5.1	6.0	8.0	13.5
Swamp Sparrow (*Melospiza georgiana*)				0.1			0.1		0.1	0.1
White-throated Sparrow (*Zonotrichia albicollis*)	0.1	1.1		0.1	1.7		0.4	0.4	2.2	1.6
Dark-eyed Junco (*Junco hyemalis*)		0.1		0.1	0.1		1.3	0.1	1.4	0.3
Irruptive species										
Purple Finch (*Carpodacus purpureus*)					0.1				0.1	0
White-winged Crossbill (*Loxia leucoptera*)	0.1			0.1	0.6	0.1^+	0.9	3.4	1.6	3.6
Pine Siskin (*Carduelis pinus*)	0.1	2.3		1.1	2.3	1.7	0.9	3.0	3.3	8.1
Evening Grosbeak (*Coccothraustes vespertinus*)				0.1		0.1	0.1	0.1	0.1	0.3
Year-round residents										
Ruffed Grouse (*Bonasa umbellus*)	0.1^+	0.1^+		0.6	0.1^+				0.2	0.7
Hairy Woodpecker (*Picoides villosus*)		0.1^+			0.1^+		0.1		0.2	0.1
Three-toed Woodpecker (*P. tridactylis*)								0.1^+	0	0.1
Pileated Woodpecker (*Dryocopus pileatus*)					0.1^+	0.6			0.1	0.6
Woodpecker species		0.1^+						0.1^+	0	0.2
Gray Jay (*Perisoreus canadensis*)			0.1		0.1^+	0.2	0.9	0.9	1.1	1.1
Black-capped Chickadee (*Parus atricapillus*)	0.6	1.1	0.6	0.6				0.9	1.2	2.6
Boreal Chickadee (*P. hudsonicus*)	0.6			0.6	1.1	1.7	0.9	1.3	2.6	3.6
Total no. of pairs	57.9	39.0	24.9	20.1	44.1	36.3	25.1	33.0		

Note 0.1 denotes visitor in 1973, possible breeder or cluster in 1990/1991; 0.1^+ is probable breeder.

APPENDIX II

ESTIMATED NUMBERS OF PAIRS/10 HA AT MAFEKING, MANITOBA CENSUS SITES

Common and scientific name	Novra 1972	Novra 1992	Steeprock Bay 1972	Steeprock Bay 1992	Bellsite 1972	Bellsite 1992	Mafeking 1972	Mafeking 1992	Total 1972	Total 1992
Long-distance migrants										
Ruby-throated Hummingbird (*Archilochus colubris*)						0.1[a]			0	0
Olive-sided Flycatcher (*Contopus borealis*)				0.1[a]				0.1[a]	0	0
Yellow-bellied Flycatcher (*Empidonax flaviventris*)			0.1				0.1	0.1	0.2	0.1
Alder Flycatcher (*E. alnorum*)		0.1[a]							0	0
Least flycatcher (*E. minimus*)	2.3	6.9		0.1		0.1[a]			2.3	7.0
Great Crested Flycatcher (*Myiarchus crinitus*)	1.7	0.1	0.1	0.1					1.8	0.2
Bank Swallow (*Riparia riparia*)						0.1			0	0.1
Veery (*Catharus fuscesens*)	4.6	5.7		0.2		0.1			4.6	6.0
Swainson's Thrush (*C. ustulatus*)	2.3	5.7	2.5	2.5		0.1[a]	1.7	0.2	6.5	8.4
Solitary Vireo (*Vireo solitarius*)			1.9	0.2	0.7	0.1	1.1	0.9	3.7	1.2
Warbling Vireo (*V. gilvus*)	0.1			0.1					0.1	0.1
Philadelphia Vireo (*V. philadelphicus*)	2.9	1.7		0.6					2.9	2.3
Red-eyed Vireo (*V. olivaceus*)	8.0	16.0		3.2		1.7		0.1[a]	8.0	20.9
Tennessee Warbler (*Vermivora peregrina*)	1.1	1.1	0.2	0.6	0.3		2.3		3.9	1.7
Orange-crowned Warbler (*V. celata*)		0.1							0	0.1
Nashville Warbler (*V. ruficapilla*)		0.1		0.6	0.1	1.7	2.3	0.9	2.4	3.3
Chestnut-sided Warbler (*Dendroica philadelphia*)	0.6	0.6	0.1	0.6		0.9			0.7	2.1
Magnolia Warbler (*D. magnolia*)		0.6	6.3	8.3		0.3			6.3	9.2
Cape May Warbler (*D. tigrina*)		0.1		0.2				0.6	0	0.9
Black-throated Green Warbler (*D. virens*)		0.6	3.8	3.2					3.8	3.8
Blackburnian Warbler (*D. fusca*)			1.3	0.6				0.1	1.3	0.7
Palm Warbler (*D. palmarum*)						0.2			0	0.2
Bay-breasted Warbler (*D. castanea*)			1.3	0.6			0.6	0.1	1.9	0.7
Black-and-white Warbler (*Mniotilta varia*)	4.0	0.6	0.1	2.5					4.1	3.1
American Redstart (*Setophaga ruticilla*)	19.4	18.0	0.6	6.3					20.0	24.3
Ovenbird (*Seiurus aurocapillus*)	6.3	6.9	1.0	4.4		2.2			7.3	13.5
Northern Waterthrush (*S. noveboracensis*)	1.7	1.1		0.1[a]		0.1[a]			1.7	1.1
Connecticut Warbler (*Oporornis agilis*)				0.1	0.7	0.3		0.9	0.7	1.3
Mourning Warbler (*O. philadelphia*)	0.1	0.6	1.0	0.2					1.1	0.8
Common Yellowthroat (*Geothlypis trichas*)		0.2		0.1			0.6		0.6	0.1
Canada Warbler (*Wilsonia canadensis*)	1.7	8.6	4.1	3.8				0.1[a]	5.8	12.4
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1.1	1.7		0.6		0.1			1.1	2.4
Chipping Sparrow (*Spizella passerina*)			1.0	1.9	3.4	3.4	1.1	1.7	5.5	7.0
Clay-colored Sparrow (*S. pallida*)						0.5			0	0.5
Lincoln's Sparrow (*Melospiza lincolnii*)								0.2	0	0.2

APPENDIX II
CONTINUED

Common and scientific name	Novra		Steeprock Bay		Bellsite		Mafeking		Total	
	1972	1992	1972	1992	1972	1992	1972	1992	1972	1992
Short-distance migrants										
Mourning dove (*Zenaida macroura*)		0.1[a]				0.1		0.1	0	0.2
Yellow-bellied Sapsucker (*Sphyrapicus varius*)		0.1[a]	0.1						0.1	0
Northern Flicker (*Colaptes auratus*)				0.1[a]			0.1		0.1	0
Blue Jay (*Cyanocitta cristata*)		0.1[a]		0.1[a]		0.1[a]			0	0
Red-breasted Nuthatch (*Sitta canadensis*)			1.9	0.2				0.6	1.9	0.8
Brown Creeper (*Certhia americana*)				0.2			0.3		0.3	0.2
Winter Wren (*Troglodytes troglodytes*)			0.6	1.3			0.3	0.3	0.9	1.6
Golden-crowned Kinglet (*Regulus satrapa*)			0.1	0.6		0.3	1.7	1.7	1.8	2.6
Ruby-crowned Kinglet (*R. calendula*)				2.5	0.1		4.0	3.4	4.1	5.9
Hermit Thrush (*Catharus guttatus*)					1.7	2.4			1.7	2.4
American Robin (*Turdus migratorius*)	0.1					0.1[a]		0.1[a]	0.1	0
Cedar Waxwing (*Bombycilla cedrorum*)					0.7				0.7	0
Yellow-rumped Warbler (*Dendroica coronata*)		0.1	1.3	3.2	2.4	0.7	2.3	2.3	6.0	6.3
Vesper Sparrow (*Pooecetes gramineus*)					0.3	0.1[a]			0.3	0.1
Song Sparrow (*Melospiza melodia*)						0.2			0	0.2
White-throated Sparrow (*Zonotrichia albicollis*)		1.4	1.9	3.5		0.9		0.1	1.9	5.9
Dark-eyed Junco (*Junco hyemalis*)			0.1		1.7	0.3	0.3		2.3	0.3
Brown-headed Cowbird (*Molothrus ater*)	0.1	0.1[a]							0.1	0
American Goldfinch (*Carduelis tristis*)		0.1				0.1[a]			0.1	0.1
Irruptive species										
Purple finch (*Carpodacus purpureus*)	0.1	0.6	0.2	0.1[a]		0.1			0.3	0.7
White-winged Crossbill (*Loxia leucoptera*)		1.1				0.1			0	0.1
Pine Siskin (*Carduelis pinus*)				0.1					0	0.1
Evening Grosbeak (*Coccothraustes vespertinus*)		2.0				0.3		0.1	0	3.1
Year-round residents										
Spruce Grouse (*Dendragapus canadensis*)		0.1		0.1			0.3	0.3	0.3	0.5
Ruffed Grouse (*Bonasa umbellus*)	0.1								0.1	0
Downy Woodpecker (*Picoides pubescens*)	0.6			0.1					0.6	0.1
Hairy Woodpecker (*P. villosus*)		0.6	0.3	1.0		0.3			0.3	1.9
Black-backed Woodpecker (*P. arcticus*)				0.6					0	0.7

APPENDIX II
CONTINUED

Common and scientific name	Novra		Steeprock Bay		Bellsite		Mafeking		Total	
	1972	1992	1972	1992	1972	1992	1972	1992	1972	1992
Three-toed Woodpecker (*P. tridactylus*)								0.6	0	0.6
Pileated Woodpecker (*Dryocopus pileatus*)				0.6					0	0.6
Black-capped Chickadee (*Parus atricapillus*)	0.1	1.1		0.2	0.2	0.2		0.6	0.3	2.1
Boreal Chickadee (*P. hudsonicus*)			0.1	0.2		0.1	1.1	0.6	1.2	0.9
Gray Jay (*Perisoreus canadensis*)		0.2	0.1	0.6	0.1		0.6	0.3	0.8	1.1
White-breasted Nuthatch (*Sitta carolinensis*)	0.1	0.2							0.1	0.2
Total no. breeding pairs	59.1	83.9	32.1	57.1	12.4	19.2	20.9	17.1		

Note 0.1 denotes visitor in 1972, possible breeding or cluster in 1992; 0.1^{+} is probable breeder; ^{a} = birds recorded at edge of plot, possible visitors or associated with other stand type (excluded from totals).