

## Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest

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The boreal mixed-wood forest of northern Alberta, Canada is characterized by a mosaic of deciduous and coniferous forest patches. Recently, the deciduous portion of the forest was allocated for industrial logging. Widespread habitat loss and fragmentation may negatively affect birds and other wildlife. Most research on the effects of habitat loss on bird abundance has focussed on the forest as a patch or island in a matrix of non-habitat, but some species of songbird may use both the forest patch and the matrix. We hypothesized that some species of songbird might be able to compensate for a loss of deciduous forest by moving into other habitat types (termed “habitat compensation”). We report on a replicated field investigation in which we assessed the response of songbirds to commercial timber harvest by first examining their abundance within deciduous forest only, and then adding the clearcuts and coniferous forest in the surrounding areas to the analysis for a broader, landscape view of the system. Bird communities in deciduous and coniferous habitats had significant overlap in species composition; there was less overlap between forest and clearcuts. The shift from patch-centred to landscape sampling altered our interpretation of over half of the most common species’ responses to logging in at least one year, suggesting that habitat compensation may have been occurring. However, significant variation in responses of species was observed between the two study areas. Our past reliance on island biogeographic and other single habitat approaches may be inappropriate for this system, and we stress that a broad, landscape view is required to properly assess and interpret species’ responses to habitat loss and fragmentation.

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Habitat loss and fragmentation of previously contiguous landscapes have been a concern of conservationists for over two decades. Assessing the impact on species and communities in remnant (or fragmented) areas has been the focus of intensive scientific research for just as long (e.g. Forman et al. 1976, Wilcove et al. 1986). Landscape changes, such as a reduction in original habitat area, isolation of remaining habitat patches, and an increase in edge relative to interior habitat have all been implicated as having negative effects on some

wildlife populations (Saunders et al. 1991). Declines in several species of birds have been partially attributed to the loss and fragmentation of their breeding habitat (e.g. Whitcomb et al. 1981, Böhning-Gaese et al. 1993), and neotropical migrant songbirds appear to be particularly sensitive (Robbins et al. 1989, Morton 1992).

To date, our perception of the impacts of habitat fragmentation has been heavily based on the theory of island biogeography (MacArthur and Wilson 1967). This theory has dominated our decisions about which

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variables to measure (Wiens 1994), and has also kept us focussed on the somewhat simplistic concept of the 'patch', as opposed to the whole landscape, in the design of our experiments. The more recent development of metapopulation theory has tended to reinforce this single habitat approach (e.g. Harrison 1994). Researchers have often viewed habitat patches in isolation from the surrounding landscape. However, habitat fragments typically are not embedded in a totally inhospitable matrix as are true islands (Wiens 1994). This may be particularly true in dynamic forest landscapes, such as those harvested for timber, where new successional habitats have been introduced and where logging causes a perforated, rather than a truly fragmented, landscape (*sensu* Forman 1997).

The boreal forest is naturally patchy and particular habitat types are spatially distinct even without human intervention (Hansson 1992). A consideration of only one habitat type may be misleading because many bird species use multiple habitats, and some individuals may even include more than one habitat type within their territory (Haila et al. 1989). Some species may compensate for a loss (or fragmentation) of their preferred habitat by shifting to less preferred habitat types, a process we term "habitat compensation". If demographic rates are habitat-specific (Pulliam and Danielson 1991), then habitats occupied due to compensation may function as population sinks. Alternatively, bird species may not recognize the habitat classifications defined by resource managers or researchers, making a focus on only one habitat type inappropriate. Habitat boundaries that we perceive may not be distinct in terms of ecological function (Wiens et al. 1985), and may be partially or fully permeable to birds. Studies focussed on only one focal habitat type could miss a significant portion of the habitat available to the boreal bird community and may misrepresent response patterns of birds to forest loss. Thus, only with a broader, landscape view can we hope to detect and properly interpret changes in bird communities following forest loss and fragmentation.

The issue of spatial scale has received considerable attention in recent years. Many specific factors, associated with adopting a larger scale of reference, have been shown to influence our interpretation of bird communities. Regional population trends, and the landscape context of studied habitat patches, for example, have been shown to be significant in understanding smaller scale patterns in bird communities (e.g. Helle 1986, Jokimäki and Huhta 1996). Studies of this nature typically are concerned with scale changes of several orders of magnitude. However, Addicott et al. (1987) and Haila et al. (1989), among others, have emphasized the potential significance of much smaller changes in study scale to ensure inclusion of all relevant habitat types in the "ecological neighborhood".

The boreal forest of western Canada, including the province of Alberta, provides breeding habitat for many neotropical migrant bird species. Over 70% of the boreal mixed-wood forest has been allocated for harvesting by commercial timber companies (Anon. 1996). In addition, forest is lost due to clearing for agriculture and for oil and gas development and production, with concomitant increase in road density. Potential loss of old growth forest and increased fragmentation of this system have raised questions about the ability of populations of some species to persist in these areas. Forest management in northern Alberta, where this study was conducted, has tended to treat the deciduous and coniferous components of the forest separately (Cumming and Armstrong 1999). Coniferous stands are harvested for both saw-logs and pulp, while deciduous forest is harvested primarily for pulp. In general, coniferous and deciduous harvest operations and management are conducted by different companies, but often on the same land base. The harvest of deciduous forests, in particular, has accelerated since 1988 with over 220 000 km<sup>2</sup> of forest now under lease to forest companies. Deciduous-dominated forest is harvested using a two or three pass clearcutting system whereby equal amounts of timber are taken in a checkerboard pattern in each of two or three harvesting periods spaced at roughly 10 yr intervals (Anon. 1992). After the first harvesting pass, remnant patches of deciduous forest remain, but they are not true isolates. They are connected to either coniferous forest or harvested areas (clearcuts), both of which provide suitable habitat for some bird species. Thus, the application of an island biogeographic, or single habitat, approach to such a system is questionable, or at least limited.

This study was designed to assess the response of boreal songbirds to deciduous forest loss and the introduction of clearcuts by examining both patch-centred (i.e. focussing on the remaining deciduous forest patches) and broader landscape scales (i.e. including other forest types and clearcuts). The landscapes in question were pyrogenic and relatively undisturbed prior to harvesting of the deciduous habitat. We expected to find differences between patch and landscape-level analyses if bird species were able to compensate for loss of deciduous habitats by increasing their use of coniferous habitats and clearcuts. We posed the following two general questions: 1) does forest loss by clearcutting affect songbirds in remaining patches of deciduous forest? Here we compared bird presence and abundance in deciduous patches in a logged landscape vs those in similar sized areas embedded in continuous forest. 2) Does our interpretation of the effects of habitat loss differ when additional habitat types across the landscape (coniferous forest, clearcuts) are included in the analysis?

## Methods

### Study area

The study areas were located in the boreal mixed-wood forest region (Rowe 1972) near Calling Lake, Alberta, Canada (55°15'N, 113°19'W), about 250 km north of Edmonton (Fig. 1). The forest is dominated by deciduous stands of trembling aspen *Populus tremuloides* Michx. and balsam poplar *P. balsamifera* L. with lesser amounts of white birch *Betula papyrifera* Marsh. The principal coniferous tree species on mesic and xeric sites are white spruce *Picea glauca* (Moench) Voss and jack pine *Pinus banksiana* Lamb. Wetter sites are dominated by black spruce *Picea mariana* (Mill.) BSP and open and shrubby bogs. Mixed stands of aspen and spruce are common. A natural mosaic of deciduous, coniferous and mixed stands across the landscape is maintained by frequent disturbances such as fire and insect outbreaks and by variation in

drainage and topography. The forest habitats studied originated after fire between 1860 and 1920. Only very limited, non-industrial logging had previously occurred in these forests, but the area had been disturbed by the clearing of seismic exploration lines (roughly 6 m wide) and natural-gas well construction.

### Study design

Two pairs of logged (treatment) and unlogged (reference) areas were sampled (Fig. 2). The first pair at Quinn Creek (QC) encompassed roughly 70 km<sup>2</sup>, the second pair at Calling Lake (CL) encompassed roughly 100 km<sup>2</sup>. All sampling points were laid out to allow comparison between logged and unlogged areas within each pair of landscapes. The minimum distance between sampling locations at Quinn Creek and Calling Lake was 600 m, but was generally > 2.5 km.

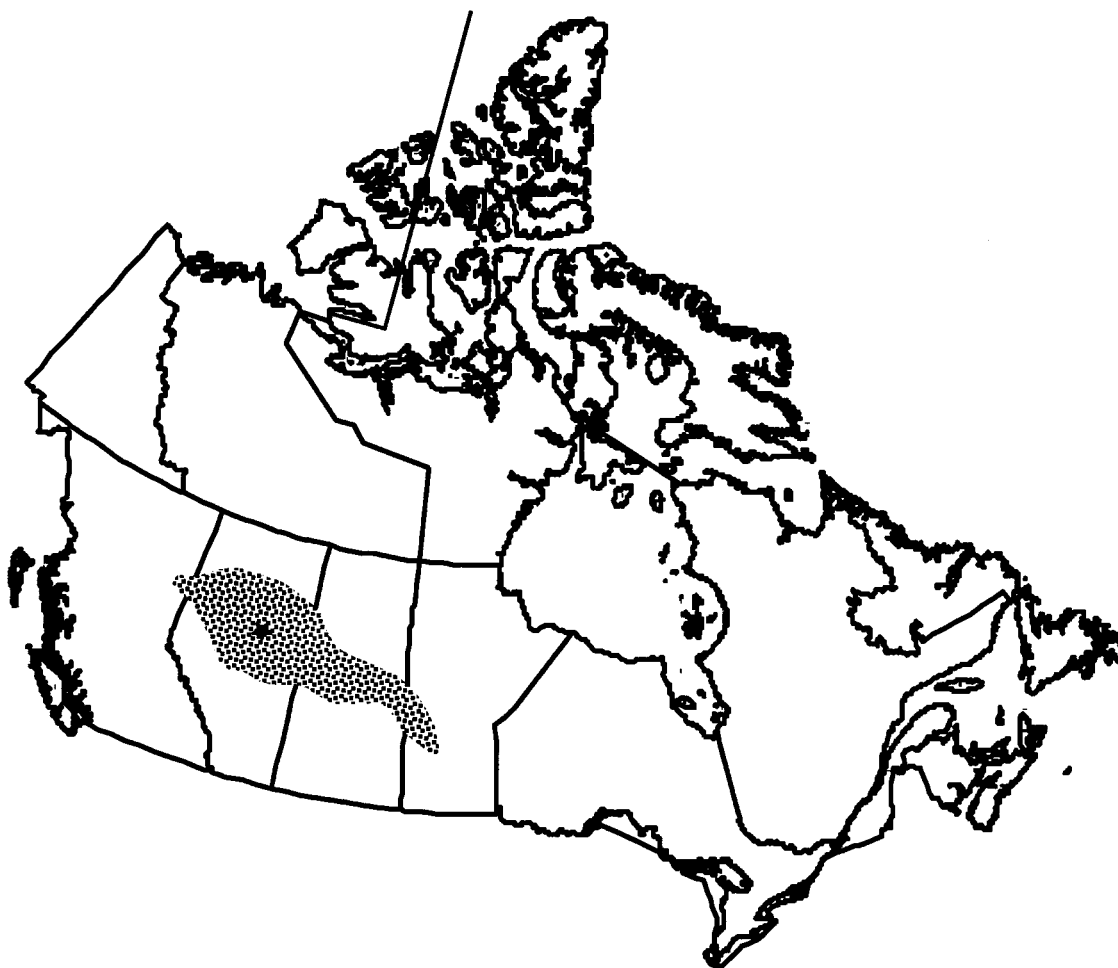


Fig. 1. Map of Canada showing extent of the boreal mixed-wood forest (stippled) and the location of study areas in Alberta (star).

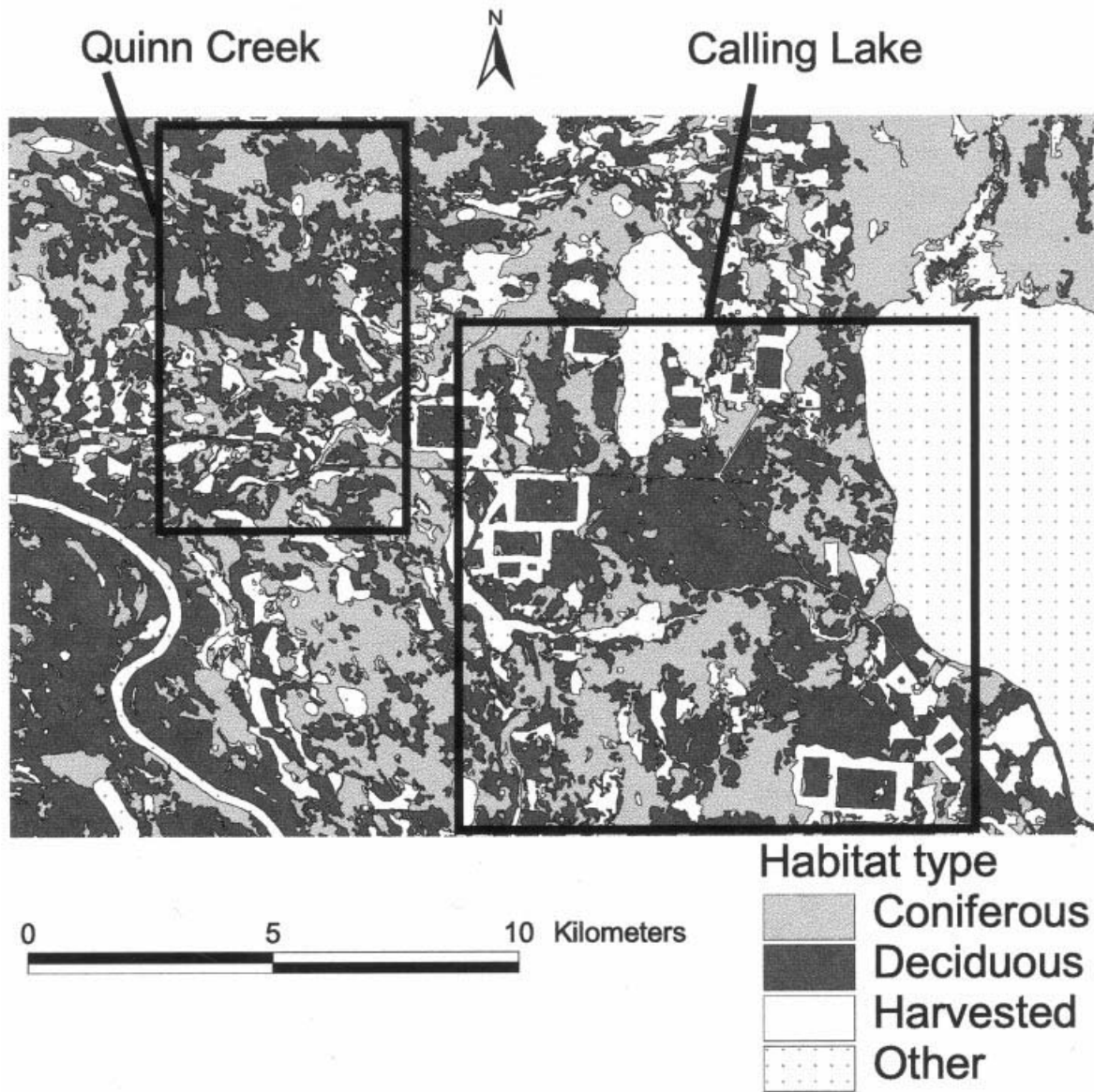


Fig. 2. Map of the Calling Lake and Quinn Creek landscapes showing the three sampled habitat types. The “Other” habitat class includes non-productive forest, wetlands, and water bodies and was not sampled for this study.

All harvesting of aspen forest occurred during the winter of 1993–1994. Data presented here for the bird communities were collected during the breeding seasons of 1994 and 1995, i.e. the first two years post-harvest. Harvesting at Quinn Creek followed a roughly checkerboard pattern; cut patches averaged about 30 ha (range 3–60 ha) with equivalent sized fragments (leave-areas) left for a second-pass harvest in about 10 yr. The treatment area at Calling Lake was experimentally harvested to leave a 200 m wide strip around rectangular forest isolates of 1, 10, 40, and 100 ha (Schmiegelow and Hannon 1993, Schmiegelow et al. 1997). Data for the current study were subsampled from the data pre-

sented in Schmiegelow et al. (1997) to match as closely as possible the spatial layout of points at Quinn Creek, plus we added additional data points from other habitat types (see below). The unlogged (reference) areas were adjacent to the logged (treatment) areas and were undisturbed except for seismic lines and one logging road in each area. Sampling locations in the reference areas were a minimum of 400 m (Quinn Creek) or 650 m (Calling Lake) from the nearest harvested stands.

Each pair of logged and unlogged areas was matched for their proportions of dominant habitat types and stand ages using Alberta Phase 3 Forest Inventory data (Anon. 1985). Detailed vegetation data were collected

at all census stations to confirm this matching of habitats. Sampling was plot-based, and all vegetation strata including canopy, subcanopy, shrub and ground cover were quantified. Analysis of the detailed data confirmed that habitats in logged and reference areas were generally well matched (Norton 1997, Schmiegelow et al. 1997). However, at Quinn Creek the reference area had a slightly higher density of shrubs than the logged area, and the logged area had a higher density of coniferous trees, particularly in the understory. See Norton (1997) and Schmiegelow et al. (1997) for full methodological details and results of deciduous forest comparisons.

Three forest bird habitat types were defined a priori: deciduous-dominated habitats composed of > 60% aspen trees by cover, clearcuts resulting from harvesting of deciduous forest, and coniferous-dominated forest stands composed of > 50% white spruce (Fig. 2). Sites characterized by black spruce were insufficiently sampled for detailed analysis, but had low bird species overlap with deciduous forest (Norton unpubl.). As the deciduous and coniferous forests we studied represent most of the commercially merchantable forest in the area, we herein refer to their combination as "All forest". In each pair of logged and reference areas, the number of bird census stations (see Data collection and analysis) was proportional to the area of deciduous, clearcut and coniferous forest habitat present in the landscape (Table 1). Stations were grouped into "sites": deciduous forest fragments, clearcuts, and patches of coniferous forest with 1–6 stations in each at a density of roughly one station per 5 ha. The size distribution of sites and the sampling locations therein were always matched between logged and reference areas, as well as their spatial configuration, whenever possible. Reference stations for clearcuts were located in additional uncut deciduous habitats in the reference areas to match the pre-harvest condition of clearcut sites. A total of 126 stations were surveyed at Quinn Creek (63 in the logged area and 63 in the reference area), and 196 stations were surveyed at Calling Lake (98 logged and 98 reference).

## Data collection and analysis

Songbirds were surveyed using a 100 m fixed-radius point-count technique, following standards recommended by Ralph et al. (1993). Stations were located 200 m apart to minimize double-counting of birds at adjacent stations. We surveyed birds at the peak of the breeding season each year (late May–early July), from sunrise until 10:00 am. Trained observers were rotated among sites. Each station was visited three times in each of 1994 and 1995, at roughly 10 day intervals, for 5 min per visit. Only records of passerines and one woodpecker species were retained for analyses, as other woodpeckers, waterfowl, raptors and gallinaceous species are not appropriately censused using the point-count protocol and surveying dates used in this study. Records of transient species and questionable identifications were also removed from the data set prior to analyses.

In calculating abundance, observations were weighted according to observed behaviour: singing males were scored as 1.0, silent or calling birds as 0.5, and observed pairs and nests were scored as 2.0. Abundances at a given station were calculated as the mean abundance per census round (Schmiegelow et al. 1997). This technique is more conservative than the more common use of maximum abundance values. Bird densities were not calculated because of the requirement for accurate distance estimates for each bird detection (Blake et al. 1994).

Bird communities were compared among the three habitat types using simple rank-abundance curves. Deciduous forest communities were used as the reference point from which to establish similarities and differences in the communities of clearcut and coniferous forest sites. We used the Jaccard coefficient (Ludwig and Reynolds 1988) as a simple, interpretable index to quantitatively compare species composition of the different habitats in the two landscapes in each year. The index ranges from 0 for no overlap to 1 for total overlap. The index was calculated in each year, at both Quinn Creek and Calling Lake, between deciduous

Table 1. Proportional habitat area and sampling effort for each pair of landscapes. Proportional areas are given relative to the total area of forested plus harvested land in each landscape; the remainder of the land base is dominated by black spruce and wetland areas. Sampling distribution is shown for the logged areas only. Reference stations for clearcuts were allocated to additional aspen stands, but otherwise sampling effort was equivalent in the reference areas, except where noted.

Landscape	Year	Deciduous forest			Deciduous clearcut			Coniferous forest		
		Area	# Stns	# Sites	Area	# Stns	# Sites	Area	# Stns	# Sites
Quinn Creek	1994		34	13		14	5		10	3
	1995	45.5%	34	13	16.7%	14	5	17.5%	15	4
Calling Lake	1994		60	19		14	5		24	7
	1995	50.4%	60	19	12.7%	14	5	20.2%	10†	4

† Only coniferous forest in the logged area of Calling Lake was undersampled in 1995; a full complement of 24 stations was sampled in coniferous forest reference areas.

forest and clearcut (4 comparisons: logged areas only) and between deciduous and coniferous forest (8 comparisons: logged and reference areas). The species abundance curves were also used to qualitatively identify those species which were found in multiple habitat types and which therefore might be expected to exhibit habitat compensation.

Abundances were compared between logged and reference areas within deciduous forest only, then with coniferous forest and clearcuts included. Only the most abundant species in each landscape were analyzed to ensure a reasonable sample size for statistical testing: 10 species from Quinn Creek and 15 from Calling Lake. Generally, these were species with  $\geq 5$  detections per study area per year. Data did not meet the assumption of normality, so non-parametric Mann-Whitney U-tests were used in all cases. If abundance relationships are the same at patch and landscape scales, we can more confidently state whether a species responds positively (higher abundance in the logged areas) or negatively (higher abundance in the reference areas) to the logging. If we find a difference in abundance relationships between patch and landscape then habitat compensation may be occurring, indicating that a patch-centred perspective is not appropriate.

The species analyzed were ordered according to whether they were found predominantly in deciduous forest (deciduous species), found in both deciduous and coniferous forest (forest generalists), found predominantly in coniferous forest (coniferous species) or used forest and clearcuts (habitat generalists) (see Table 2).

We also analyzed total bird abundance on a per-station basis in both 1994 and 1995 to test whether the effects of habitat compensation by some species could be detected at the community level. Only those species detected in deciduous forest in each landscape were included. The mean number of individuals detected at each census station was tallied for each habitat type and for all habitats combined, in each of the logged and reference areas. Values were compared with t-tests because the assumption of normality was met.

We used  $\alpha = 0.1$  when interpreting the results of all statistical tests on bird data to minimize the chances of making Type II errors, which we feel can be more risky than Type I errors in applied research (e.g. Wiens and Parker 1995, Schmiegelow et al. 1997).

## Results

### Bird communities

We analyzed 15 758 detections of birds representing 57 species of songbirds, plus the yellow-bellied sapsucker (for a full list of species and scientific names see Appendix 2). Community composition was dominated by Neotropical migrants (54%) and short-distance mi-

Table 2. Summary of species' responses to treatment (deciduous habitats compared to all habitats) determined by Mann-Whitney U-tests. The treatment area in which the species had a higher abundance ( $p < 0.10$ ) is indicated (R = reference, L = logged, = no significant difference). Results are shown for 1994 and 1995 separately when a difference in response between years was detected. Species are arranged according to their range of habitat use, from deciduous forest specialists through forest generalists to coniferous forest specialists, and true habitat generalists. Species in **bold** showed a different response in both years between Deciduous and All habitats analyses in at least one of the study areas. Detailed results of statistical tests are presented in Appendix 1; species codes and scientific names are presented in Appendix 2.

Species	Quinn Creek		Difference btw areas*	Calling Lake	
	Decid	All		Decid	All
<b>AMRE</b>		†		L	=
Deciduous Species				(94) =	=
<b>LEFL</b>	R	R	↔	(95) L	L
<b>RBGR</b>	-----			(94) L	L
				(95) =	=
<b>YEWA</b>	-----			L	=
<b>COWA</b>	L	=	↔	=	=
<b>REVI</b>	R	R	↔	=	R
				(94) L	=
<b>MOWA</b>	R	R	↔	(95) =	L
<b>TEWA</b>	(94) R	=		-----	
	(95) R	R			
<b>OVEN</b>	=	R		(94) =	R
			↔	(95) R	R
<b>BINW</b>	-----			(94) =	=
				(95) =	R
<b>YRWA</b>	L	=	↔	=	=
<b>SWTH</b>	=	=		=	=
				(94) =	=
<b>RBNU</b>	-----			(95) =	R
Coniferous Species				(94) =	=
<b>WETA</b>	-----			(95) R	R
	(94) L	L		(94) =	=
<b>CHSP</b>	(95) =	L	↔	(95) R	R
Habitat					
<b>Generalists</b>	(94) R	R		(94) =	=
<b>WTSP</b>	(95) R	=	↔	(95) =	L

\* ↔ Species with a different response between Quinn Creek and Calling Lake.

† ----- Species not detected in sufficient numbers for analysis.

grants (36%). The only relatively abundant resident species was the red-breasted nuthatch. The overall species abundance distribution was heavily skewed with the 15 most abundant species in deciduous forest accounting for 80.9% of the total number of individuals. Deciduous forest bird communities in the two landscapes were similar in terms of species composition, but the slightly younger forests at Quinn Creek influenced the abundances of some species (cf. Schieck et al. 1995; Fig. 3). In particular, ovenbirds and Connecticut warblers were proportionally more abundant at Quinn Creek, while species such as the mourning warbler and American redstart had higher abundances in the older forests at Calling Lake.

Bird communities in coniferous habitats had a high degree of overlap in species composition with deciduous forest. Jaccard values expressed as percentages ranged from 50.0 to 73.9. Many of the most abundant species in both habitat types were shared, including yellow-rumped warbler, black-throated green warbler, Swain-

son's thrush, red-breasted nuthatch, and western tanager. Only seven species were found in a single habitat type, however five of these were very rare (Appendix 2).

Clearcut sites had a lower degree of overlap in species composition with deciduous forest sites. Jaccard values ranged from 21.4% to 40.0%. At both Quinn Creek and Calling Lake, only two species occurred in significant numbers in both clearcuts and deciduous forest: white-throated sparrow and chipping sparrow. Several other species found in deciduous forest were present at lower abundances in clearcuts including least flycatcher, Tennessee warbler, and mourning warbler. Five species reached their peak abundances over the landscape in clearcuts: alder flycatcher, house wren, Lincoln's sparrow, clay-coloured sparrow, and song sparrow.

Because some species were unique to clearcuts, total species richness across all habitats was slightly higher in the logged areas (49 species QC, 52 species CL) than in

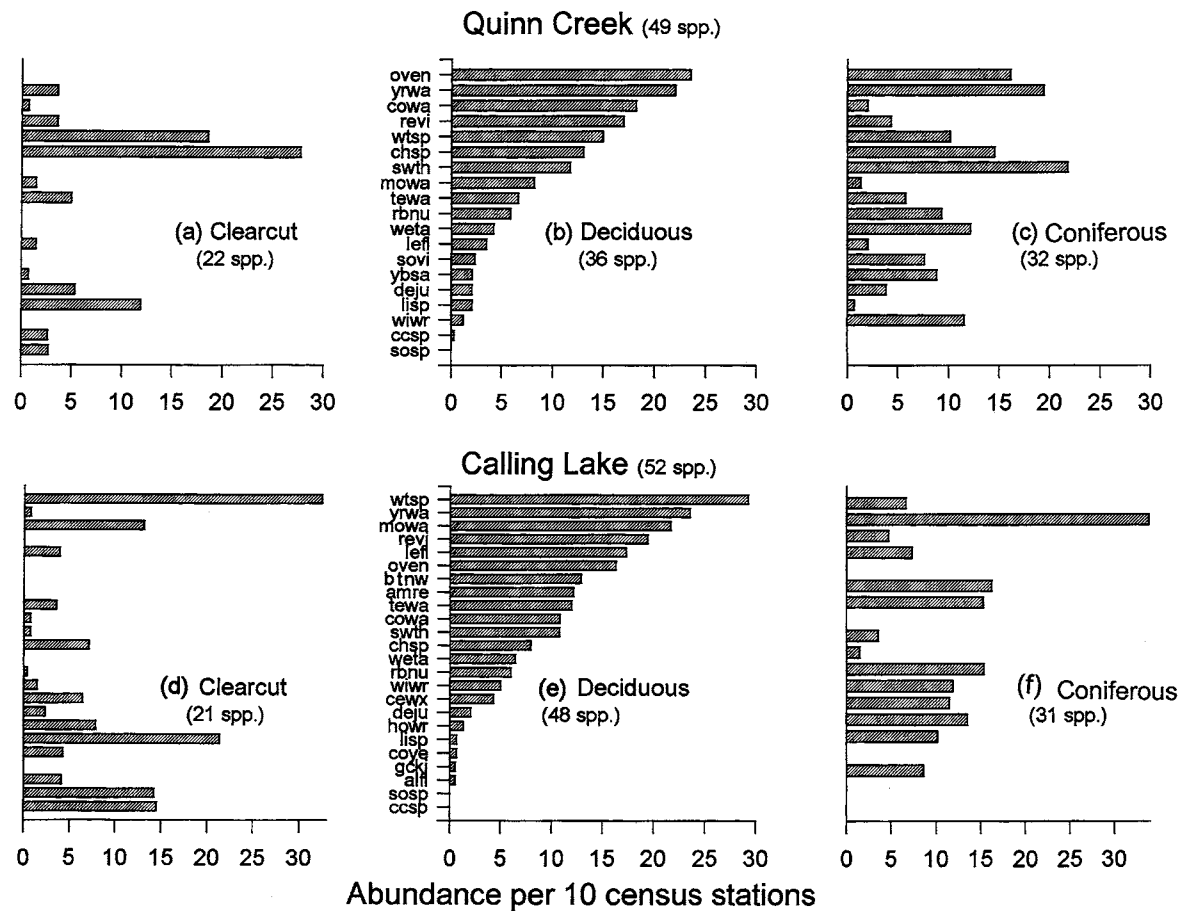


Fig. 3. Bird community profiles for three habitat types in each of the Quinn Creek and Calling Lake landscapes. Species are identified by standardized 4 letter codes after Pyle et al. (1987); see Appendix 2 for explanation. The species displayed for each landscape are a combination of the 15 most abundant species in each habitat type (1994 and 1995 pooled, logged areas only). Abundances have been standardized to 10 census stations, or roughly 50 ha, for ease of interpretation.

the reference areas (42 species QC, 50 species CL). Five species detected only in the logged areas were alder flycatcher, olive-sided flycatcher, clay-coloured sparrow, song sparrow, and LeConte's sparrow.

### Individual bird species abundances with respect to logging

#### *Patch level*

At the patch level (i.e. deciduous forest only), many species' abundances appeared to be affected by logging. Eight out of 10 species at Quinn Creek, and 8 of 15 at Calling Lake had different abundances in deciduous forest patches in the logged versus the reference areas in at least one year (Table 2, Appendix 1). Five species at Quinn Creek had higher abundances in the reference area, suggesting a negative response to logging. There was more inter-annual variation at Calling Lake, and only three species had higher abundances in the reference area in at least one year. Three species at Quinn Creek, and five at Calling Lake had higher abundances in the logged area. Differences in abundances between logged and reference areas for particular species within a study area differed by roughly 10–70% in most cases, but differed by up to 300% in some instances (e.g. least flycatcher at Quinn Creek, see Appendix 1). No species was completely lost from the logged landscape at either study site.

#### *Landscape level*

At the landscape level (i.e. all habitats), six species at Quinn Creek and six species at Calling Lake appeared to be negatively affected by logging in at least one year (seen as higher abundances in the reference areas "R" in Table 2). Two species responded negatively to logging in both study areas: red-eyed vireo and ovenbird. Only one species at Quinn Creek, chipping sparrow, responded positively to logging with higher abundances in the logged area across all habitats. For this species, the difference between logged and reference was even greater at the landscape level due to its use of clearcuts (Appendix 1). At Calling Lake, four species were more abundant in the logged landscape in at least one year: least flycatcher, mourning warbler, white-throated sparrow and, surprisingly, the rose-breasted grosbeak which, unlike the other species, was not observed singing in clearcuts (Appendix 1).

#### *Patch vs landscape views*

The apparent response of species to logging was altered with a landscape view compared to a patch-centered view in several cases. Three out of 10 species analyzed at Quinn Creek (Connecticut warbler, ovenbird, yellow-rumped warbler), and three of 15 at

Calling Lake (American redstart, yellow warbler, red-eyed vireo) exhibited a consistent (i.e. observed in both years) different pattern of abundance response to logging between analyses of "Deciduous" patches and "All habitats" (Table 2). Overall, 11 of 16 species showed a different response in at least one year at either Calling Lake or Quinn Creek (Appendix 1). Of the nine species common to both study areas, only one, Swainson's thrush, had the same pattern of response in both years and both study areas, and it showed no significant difference between logged and reference areas at either patch or landscape levels. Conversely, eight species differed between Quinn Creek and Calling Lake in the "Deciduous" vs "All habitats" analyses. Notable in this regard were least flycatcher and chipping sparrow that had opposite responses in the two study areas in at least one year.

Examining a few species in more detail (see Appendix 1), we found evidence of habitat compensation in as many as five species. Evidence for habitat compensation is seen as higher abundances in the coniferous forest in the logged areas compared with the reference areas or as significant use of the clearcuts in the logged landscapes. At Quinn Creek only Swainson's thrush showed evidence of conifer habitat compensation. At Calling Lake, four species showed signs of conifer habitat compensation (mourning warbler, black-throated green warbler, yellow-rumped warbler, western tanager) in at least one of two years. Only 10 species were observed singing in clearcuts (Appendix 1) and of these, only mourning warbler, Tennessee warbler, chipping sparrow and white-throated sparrow made significant use of the clearcuts.

### Overall bird abundance

When all deciduous forest birds were summed/station, we found that at the patch-level (deciduous forest only) responses to logging varied with year and site. Patterns detected at the patch-level differed from those at the landscape-level in the first year at both sites (Table 3). Birds did not appear to compensate for loss of deciduous habitat by moving into coniferous habitat at Quinn Creek; abundances did not differ significantly between logged and reference areas in the conifer sites (Table 3). However, there was a non-significant trend for higher use of conifer at Calling Lake in the logged landscape compared with the reference area. This, coupled with the use of clearcuts by some deciduous forest birds, resulted in similar abundances of deciduous forest birds across the logged and reference landscapes at Calling Lake (Table 3), suggesting that habitat compensation had occurred in that landscape. This may be related to the higher abundance of conifer species at Calling Lake than at Quinn Creek (Table 2, Appendix 1).

Table 3. Total abundance per census station of deciduous forest bird species compared between logged and reference areas within each habitat type, and across all habitat types. Mean number of individual birds per station (standard error) is shown. Test statistic, degrees of freedom, and associated probability from t-tests are shown for each comparison.

Habitat	Quinn Creek				Calling Lake			
	1994		1995		1994		1995	
	Logged	Reference	Logged	Reference	Logged	Reference	Logged	Reference
Deciduous	9.66 (0.40)	10.56 (0.51)	8.03 (0.38)	9.18 (0.39)	13.03 (0.47)	11.36 (0.49)	14.68 (0.50)	14.87 (0.62)
	$t_{63} = -1.40, p = 0.17$		$t_{66} = -2.10, p = 0.04$		$t_{118} = 2.46, p = 0.02$		$t_{118} = -0.24, p = 0.81$	
Coniferous	12.16 (0.91)	11.24 (0.72)	10.92 (0.65)	11.20 (0.67)	8.99 (0.46)	8.35 (0.38)	14.98 (1.66)	12.39 (0.77)
	$t_{19} = 0.80, p = 0.44$		$t_{28} = -0.29, p = 0.77$		$t_{46} = 1.07, p = 0.29$		$t_{32} = 1.62, p = 0.11$	
Clearcut	4.19 (0.57)	9.56 (0.75)	4.67 (0.55)	8.64 (0.52)	2.86 (0.53)	15.04 (0.93)	11.29 (1.01)	17.44 (0.71)
	$t_{24} = -5.81, p < 0.001$		$t_{26} = -5.26, p < 0.001$		$t_{26} = -11.35, p < 0.001$		$t_{26} = -5.01, p < 0.001$	
All habitats	8.77 (0.47)	10.47 (0.37)	7.97 (0.39)	9.54 (0.31)	10.58 (0.48)	11.15 (0.39)	14.16 (0.46)	14.63 (0.46)
	$t_{120} = -2.80, p = 0.006†$		$t_{124} = -3.16, p = 0.002$		$t_{194} = -0.91, p = 0.37$		$t_{180} = -0.73, p = 0.47*$	

† Coniferous forest habitats were undersampled at Quinn Creek in 1994.

\* Coniferous forest habitats were undersampled in the logged area at Calling Lake in 1995.

## Discussion

Bird species composition and abundances in a local area are affected by factors at numerous scales ranging from the availability of source pools of species at biogeographic or regional scales (e.g. Helle 1986, Wiens et al. 1987, Virkkala 1991) to habitat structure at the landscape scale (i.e. matrix composition, landscape forest cover; Askins et al. 1987, Virkkala 1991, Wiens 1994, McGarigal and McComb 1995, Edenius and Elmerberg 1996, Jokimäki and Huhta 1996, Sisk et al. 1997) to stand or territory-level habitat characteristics (e.g. Virkkala 1991, Jokimäki and Huhta 1996, Song 1998). Wiens et al. (1987) stressed the need to conduct studies at several nested scales. The design used in our study allowed us to examine the significance of increasing the spatial scale beyond a single habitat by adding sampling stations in habitats which would typically be considered "matrix" (Wiens 1994). The absolute sizes of our study areas were not increased by the additional sampling, and in this our study differed from others which have considered scale ranges of orders of magnitude. However, we incorporated elements of both approaches by explicitly sampling bird communities over a broader range of habitats within our landscapes.

### Overall effects of forest fragmentation and loss

The absence of strong and consistent negative effects of adjacent logging on species' abundance at the deciduous forest-patch and landscape levels was consistent with other studies done in this system (Norton 1997, Schmiegelow et al. 1997). The logged landscapes we worked in lie somewhere between "perforated" and "fragmented" on the continuum of Forman (1997). Hence, our landscapes may be below the forest cover/fragmentation threshold at which many species may start to show decreased abundance in response to re-

duced patch size and increased isolation (Andrén 1994, With and Crist 1995, Edenius and Elmerberg 1996).

### Patch vs landscape perspectives

Our intent was to investigate how the interpretation of responses of boreal forest songbirds to forest loss by clearcut logging might differ between a patch-centred and a broader, landscape perspective. With a patch-centred analysis, 3–5 species appeared to be negatively affected by logging, while up to 5 had higher abundances in the logged areas, although results differed between the two pairs of landscapes under study. The analysis at the landscape level altered our interpretation of six species' responses to habitat loss compared to the patch-centred approach. When total bird abundance was analysed in a similar way, we again found differences in patterns detected at the patch vs the landscape, with more evidence for habitat compensation in the conifer forest at Calling Lake, the area with more conifer species.

Many species of boreal songbirds utilize a variety of vegetation types or habitats (Welsh and Loughheed 1996). A number of these species appeared to show evidence of habitat compensation in our study (i.e. showed a different response between Deciduous (patch-level) and All habitats (landscape-level) analyses; bold in Appendix 1). For species that utilize more than one habitat type, or to which habitat type boundaries are to some degree permeable (Wiens et al. 1985), total population size will be a function of the whole landscape matrix. Aspen forest fragments in the industrial forest landscape of northern Alberta are not true habitat islands because much other forest remains after logging. In addition, cutblocks may be used by some species as they regenerate. The age distribution of forest stands changes but the total amount of forest area remains

more or less constant. Hence, analytical approaches based on island biogeography theory, if strictly patch-centred, may be inappropriate in heterogeneous landscapes, such as the boreal forest.

Our definition of "habitat type" was based on the age and canopy composition classes of existing forest vegetation mapping. This sort of anthropocentric bias has been recognized as an important problem in ecological research (e.g. Morris 1987, Addicott et al. 1987). Knight and Morris (1996) provided dramatic evidence of this by showing that a population of voles (*Clethrionomys gapperi*) responded neither to the two habitats recognized by the researchers, nor to the 7 habitats classified by remote sensing, but to three habitat classes. The results we obtained also suggest that human-defined habitats may not be relevant to the bird species under study. Our sampling design appeared to be sufficient for forest-dependent species, but the overlap of a few species between clearcut and bog habitats (Norton unpubl.) suggests that for 3 or 4 species, we still were not sampling their full range of habitats.

We recognize that maintenance of species' abundance in an altered landscape over the short-term does not necessarily imply a healthy long-term prognosis for the population. Detailed studies of red-eyed vireos and ovenbirds conducted elsewhere have found populations in fragmented areas to have lower viability (Gibbs and Faaborg 1990, Villard et al. 1993, Donovan et al. 1995). Further, alternative habitats such as coniferous forest may represent population sinks if species suffer lower reproductive success or higher mortality in those areas. Monitoring of populations is continuing at Calling Lake and these data should help assess the longer-term viability of populations. In our study areas, conversion of old growth forest to rotation-aged "mature" forest stands will result in an overall loss and fragmentation of old stands. Conservation concerns over the longer-term may be more connected with overall habitat loss than with fragmentation per se (e.g. Fahrig 1997); that is, loss of absolute amount of forest habitat may be more important than reduced area of forest patches or patch isolation.

### **Landscape replication and spatial and temporal variation**

Few studies conducted at this scale have included landscape replication. The lack of concordance in species' responses between the Quinn Creek and Calling Lake study areas, given their proximity and the relatively narrow range of habitats included in our analyses, was surprising. Although both landscapes provided evidence for habitat compensation and for the importance of sampling entire landscapes, the particular species affected, and their apparent response to logging differed between locations and years. This suggests that pro-

cesses acting at other scales (e.g. regional abundance of species, landscape differences in structure/composition, or local differences in habitat composition and structure) may be more important in explaining species' abundances than the effect of adjacent harvesting. For example, annual variation in total abundance of songbirds in the control area of Calling Lake was ~40% over 6 yr (Schmiegelow and Hannon in press) with species' abundance varying independently (Hannon and Schmiegelow unpubl.). Since the majority of the bird community is composed of neotropical migrants, biogeographic-scale processes may be at work. Secondly, the pattern of logging was different in the two areas, with smaller, more connected fragments at Quinn Creek, and larger, more isolated fragments at Calling Lake (Fig. 2). We tried to control for this in the way the data were subsampled from Calling Lake, but cannot rule out the possibility that the different logging patterns may have had some effect on responses to forest loss. Third, differences in vegetation between the two areas may have played a role. For example, the aspen stands at Calling Lake tended to be older and have more spruce in them than those at Quinn Creek and the bird communities had higher species richness and abundances/station over all habitats (Table 3). Hence, differences between Quinn Creek and Calling Lake in levels of population saturation and/or competition for sites with other species could have altered species' responses between landscapes. In a study in an adjacent area, Song (1998) documented that abundance of songbird species was more accurately predicted by vegetation structure at the stand level than by proximity to natural or clearcut edges.

### **Conclusions and implications**

Our results support the need to take an integrated and broad-scale approach to forest management (i.e. Petit et al. 1995). We focussed on deciduous forest harvesting, but the conifer-dominated habitats in the area are also being harvested by other companies, and harvesting plans for conifer and deciduous areas are essentially designed separately. The overlap and apparent connectedness of bird communities in these two forest types suggest that all harvesting operations should be considered in designing forest management plans where one objective is the maintenance of biodiversity. In addition, the spatial and temporal variation in apparent response to forest loss highlight the need for 1) further replication at the landscape scale to encompass a wider range of landscape variation, and 2) caution about generalizing too widely from relatively localized studies.

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**Appendix 1.** Analyses of individual species' abundances by habitat type and across all habitat types. Mean abundance of each species per census station in each habitat type is shown. Species are arranged as in Table 2, from deciduous forest specialists through forest generalists to coniferous forest species, and habitat generalists. Test statistics and associated probabilities are from Mann-Whitney U-tests; only test results for cases with both cells non-zero and at least 5 birds detected are presented. For sample sizes see Table 1. Species in **bold** had a different apparent response to logging between Deciduous and All habitats analyses in at least one year at either Quinn Creek or Calling Lake.

Species	Year	Calling Lake											
		Quinn Creek			Deciduous			Coniferous†			All habitats		
		Logged	Ref	U	Logged	Ref	U	Logged	Ref	U	Logged	Ref	U
<b>AMRE</b>	1994	0.14	0.49	U = 387, p = 0.01	0.66	0.33	U = 1432, p = 0.03	0	0	0	0.41	0.44	U = 4762, p = 0.90
	1995	0.21	0.44	U = 511, p = 0.24	0.56	0.32	U = 1493, p = 0.05	0	0	0	0.40	0.28	U = 3751, p = 0.17
LEFL	1994	0.14	0.49	U = 387, p = 0.01	0.72	0.48	U = 567, p = 0.17	0	0	0	0.44	0.44	U = 4689, p = 0.73
	1995	0.21	0.44	U = 511, p = 0.24	1.02	0.53	U = 1360, p = 0.01	0	0.39	1.46	0.79	0.53	U = 3540, p = 0.06
RBGR	1994	0.14	0.49	U = 387, p = 0.01	0.46	0.15	U = 1269, p = 0.001	0	0	0	0.28	0.14	U = 4127, p = 0.02
	1995	0.21	0.44	U = 511, p = 0.24	0.42	0.51	U = 1704, p = 0.56	0	0.17	0	0.30	0.43	U = 3667, p = 0.12
<b>YEWA</b>	1994	0.14	0.49	U = 387, p = 0.01	0.54	0.24	U = 1367, p = 0.01	0.04	0	0.66	0.34	0.24	U = 4451, p = 0.24
	1995	0.21	0.44	U = 511, p = 0.24	0.53	0.37	U = 1473, p = 0.04	0	0	0.95	0.38	0.36	U = 3904, p = 0.45
<b>COWA</b>	1994	0.99	0.70	U = 402, p = 0.08	0.58	0.55	U = 1795, p = 0.94	0.04	0.13	0	0.36	0.41	U = 4511, p = 0.36
	1995	0.84	0.58	U = 437, p = 0.06	0.51	0.65	U = 1586, p = 0.21	0.15	0	0.07	0.39	0.42	U = 3995, p = 0.68
<b>REVI</b>	1994	0.95	1.25	U = 372, p = 0.03	0.91	0.91	U = 1792, p = 0.96	0.27	0.40	0	0.62	0.78	U = 4133, p = 0.07
	1995	0.76	1.07	U = 417, p = 0.04	1.03	1.07	U = 1782, p = 0.92	0.60	0.50	0	0.81	1.01	U = 3599, p = 0.13
<b>MOWA</b>	1994	0.50	0.95	U = 307, p = 0.002	1.04	0.74	U = 1112, p < 0.001	0.04	0.04	0.07	1.30	0.69	U = 4745, p = 0.88
	1995	0.32	0.96	U = 274, p < 0.001	1.21	0.94	U = 784, p < 0.001	0.70	0.13	1.24	1.45	1.06	U = 3256, p = 0.01
<b>TEWA</b>	1994	0.15	0.39	U = 415, p = 0.05	0.07	0.24	U = 1703, p = 0.27	0.04	0.04	0.29	0.77	0.77	U = 379, p = 0.01
	1995	0.51	0.86	U = 379, p = 0.01	0.51	0.85	U = 78.0, p = 0.12	0.29	0.29	0.29	0.29	0.29	U = 78.0, p = 0.12

Appendix 1. (Continued)

Species	Year	Calling Lake															
		Quinn Creek						Calling Lake									
		Deciduous		Coniferous†		Clearcut		All habitats		Deciduous		Coniferous‡		Clearcut		All habitats	
Logged	Ref	Logged	Ref	Logged	Ref	Logged	Ref	Logged	Ref	Logged	Ref	Logged	Ref	Logged	Ref		
<b>OVEN</b>	1994	1.17	1.33	0.93	1.15	0	1.47	0.84	1.24	0.75	0.99	0.68	0.78	0	0.55	0.62	0.87
		U = 424, p = 0.16		U = 43.0, p = 0.35			U = 1210, p < 0.001				U = 1520, p = 0.12		U = 251, p = 0.41			U = 3892, p = 0.02	
	1995	1.19	1.10	0.99	1.32	0	1.41	0.88	1.22	0.89	1.41	1.14	1.14	0	0.36	0.77	1.19
		U = 541, p = 0.62		U = 65.0, p = 0.04			U = 1363, p = 0.002				U = 1152, p < 0.001		U = 115, p = 0.85			U = 2865, p < 0.001	
<b>BTNW</b>	1994									0.65	0.68	0.73	0.38	0	0.93	0.58	0.64
	1995									U = 1767, p = 0.85		U = 200, p = 0.04				U = 4505, p = 0.41	
<b>YRWA</b>	1994	1.02	0.66	1.13	1.33	0.36	0.58	0.88	0.74	1.09	1.07	1.60	1.38	0	1.21	1.06	1.17
		U = 369, p = 0.02		U = 32.0, p = 0.07			U = 1770, p = 0.62				U = 1798, p = 0.99		U = 210, p = 0.1			U = 4407, p = 0.30	
	1995	1.19	0.76	1.19	0.77	0	0.80	0.92	0.77	1.27	1.26	1.92	1.54	0.07	1.16	1.15	1.31
		U = 332, p = 0.001		U = 75.5, p = 0.09			U = 1697, p = 0.12				U = 1761, p = 0.83		U = 109, p = 0.68		U = 25, p < 0.001	U = 3617, p = 0.15	
<b>SWTH</b>	1994	0.51	0.49	1.53	1.30	0	0.25	0.56	0.57	0.45	0.32	0.56	0.84	0	0.64	0.41	0.49
		U = 504, p = 0.73		U = 34.0, p = 0.11			U = 1671, p = 0.29				U = 1578, p = 0.17		U = 193, p = 0.04			U = 4461, p = 0.34	
	1995	0.38	0.52	1.15	0.76	0	0.21	0.48	0.51	0.63	0.55	1.27	1.20	0.07	0.44	0.61	0.69
		U = 504, p = 0.31		U = 60.5, p = 0.03			U = 1887, p = 0.61				U = 1649, p = 0.40		U = 118, p = 0.92		U = 69, p = 0.07	U = 3803, p = 0.35	
<b>RBNU</b>	1994									0.51	0.48	0.58	0.67	0	0.46	0.53	0.53
	1995									U = 1787, p = 0.94		U = 261, p = 0.53				U = 4392, p = 0.24	
<b>WETA</b>	1994									0.10	0.21	0.90	0.79	0.04	0.07	0.18	0.33
											U = 1625, p = 0.12		U = 112, p = 0.73			U = 3586, p = 0.04	
	1995									0.46	0.40	0.58	0.32	0	0.63	0.42	0.41
										U = 1706, p = 0.56		U = 219, p = 0.11			U = 4772, p = 0.93		
<b>CHSP</b>	1994	0.87	0.24	0.83	1.10	1.59	0.07	1.03	0.34	0.39	0.33	0.51	0.39	0.29	0.46	0.40	0.36
		U = 252, p < 0.001		U = 45, p = 0.38			U = 1.5, p < 0.001				U = 1691, p = 0.49		U = 260, p = 0.50		U = 87, p = 0.54	U = 4597, p = 0.54	
	1995	0.44	0.26	0.90	0.80	1.19	0.07	0.72	0.35	0.41	0.80	0.80	0.77	0.43	0.50	0.46	0.75
		U = 484, p = 0.16		U = 104, p = 0.67			U = 18, p < 0.001				U = 1300, p = 0.004		U = 115, p = 0.84		U = 88, p = 0.60	U = 3230, p = 0.006	
<b>WTSP</b>	1994	0.93	1.26	0.65	0.35	0.54	1.10	0.79	1.06	1.39	1.33	0.24	0.29	1.01	1.81	1.05	1.14
		U = 358, p = 0.02		U = 37, p = 0.16			U = 20, p < 0.001				U = 1657, p = 0.45				U = 35, p = 0.004	U = 4559, p = 0.53	
	1995	0.56	0.80	0.59	0.32	1.31	0.91	0.74	0.71	1.54	1.38	0.56	0.63	2.24	1.70	1.54	1.24
		U = 442, p = 0.08		92, p = 0.32			U = 51, p = 0.03				U = 1566, p = 0.22		U = 113, p = 0.78		U = 70, p = 0.18	U = 3373, p = 0.04	

† At Quinn Creek only, 1994 coniferous forest habitats were undersampled in both logged and reference areas.

‡ At Calling Lake only, 1995 coniferous habitats in the logged area were undersampled.

**Appendix 2.** Total weighted abundances of all bird species used in analyses. Abundances are pooled across years (1994 and 1995) and landscapes (Quinn Creek and Calling Lake). Scientific names follow Anon. (1998); codes are standardized after Pyle et al. (1987) as used in Fig. 3. Sample sizes indicated are the total number of census stations for each habitat type in Quinn Creek and Calling Lake combined.

Common name	Scientific name	Code	Deciduous n = 216†	Coniferous n = 78*	Clearcut n = 28
White-throated sparrow	<i>Zonotrichia albicollis</i>	wtsp	536.1	56.9	71.5
Yellow-rumped warbler	<i>Dendroica coronata</i>	yrwa	454.5	183.0	6.0
Ovenbird	<i>Seiurus aurocapillus</i>	oven	450.8	130.3	0.0
Red-eyed vireo	<i>Vireo olivaceus</i>	revi	439.4	45.0	5.0
Mourning warbler	<i>Oporornis philadelphia</i>	mowa	388.1	24.5	20.3
Connecticut warbler	<i>Oporornis agilis</i>	cowa	263.7	9.5	2.0
Tennessee warbler	<i>Vermivora peregrina</i>	tewa	262.3	40.8	12.0
Least flycatcher	<i>Empidonax minimus</i>	lefl	249.2	6.0	7.5
Black-throated green warbler	<i>Dendroica virens</i>	btwn	223.2	65.5	0.0
Swainson's thrush	<i>Catharus ustulatus</i>	swth	202.7	132.3	1.0
Chipping sparrow	<i>Spizella passerina</i>	chsp	192.3	92.8	48.8
American redstart	<i>Setophaga ruticilla</i>	amre	174.2	2.0	2.0
Yellow warbler	<i>Dendroica petechia</i>	yewa	150.0	2.0	0.0
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	rbgr	132.7	6.0	0.0
Red-breasted nuthatch	<i>Sitta canadensis</i>	rbnu	118.5	97.0	0.5
Western tanager	<i>Piranga ludoviciana</i>	weta	110.0	75.3	0.0
Winter wren	<i>Troglodytes troglodytes</i>	wiwr	86.5	73.8	2.0
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	ybsa	86.4	36.8	1.0
Brown creeper	<i>Certhia americana</i>	brcr	62.8	40.5	0.0
Warbling vireo	<i>Vireo gilvus</i>	wavi	52.0	7.0	0.0
Blue-headed vireo	<i>Vireo solitarius</i>	sovi	51.0	60.0	0.0
Black-capped chickadee	<i>Poecile atricapillus</i>	bcch	48.0	9.5	1.5
American robin	<i>Turdus migratorius</i>	amro	44.0	0.0	0.8
Hermit thrush	<i>Catharus guttatus</i>	heth	38.8	9.0	0.0
Cedar waxwing	<i>Bombycilla cedrorum</i>	cewx	35.0	1.0	9.0
Brown-headed cowbird	<i>Molothrus ater</i>	bhco	34.6	0.8	2.5
Dark-eyed junco	<i>Junco hyemalis</i>	deju	32.5	30.4	10.8
Lincoln's sparrow	<i>Melospiza lincolnii</i>	lisp	27.0	1.0	46.5
Philadelphia vireo	<i>Vireo philadelphicus</i>	phvi	25.0	2.0	0.0
Magnolia warbler	<i>Dendroica magnolia</i>	mawa	21.0	6.0	0.0
Ruby-crowned kinglet	<i>Regulus calendula</i>	rcki	20.5	19.0	0.0
Black and white warbler	<i>Mniotilta varia</i>	bawa	19.0	9.0	0.0
Golden-crowned kinglet	<i>Regulus satrapa</i>	gcki	15.3	67.1	0.0
Blackpoll warbler	<i>Dendroica striata</i>	bpwa	14.0	3.0	0.0
Western wood pewee	<i>Contopus sordidulus</i>	wwpe	13.7	2.0	2.0
Canada warbler	<i>Wilsonia canadensis</i>	cawa	11.5	1.0	0.0
House wren	<i>Troglodytes aedon</i>	howr	11.0	0.0	13.0
Pine siskin	<i>Carduelis pinus</i>	pisi	8.5	7.5	0.0
Boreal chickadee	<i>Parus hudsonicus</i>	boch	7.5	15.3	0.0
Common yellowthroat	<i>Geothlypis trichas</i>	coye	5.0	0.0	6.0
Eastern phoebe	<i>Sayornis phoebe</i>	eaph	5.0	0.0	0.0
Baltimore oriole	<i>Icterus galbula</i>	noor	5.0	2.0	0.0
Purple finch	<i>Carpodacus purpureus</i>	pufi	5.0	4.0	0.0
Alder flycatcher	<i>Empidonax alnorum</i>	alfl	4.0	0.0	6.8
Cape May warbler	<i>Dendroica tigrina</i>	cmwa	3.0	13.0	1.0
Bay-breasted warbler	<i>Dendroica castanea</i>	bbwa	2.0	29.0	0.0
Orange-crowned warbler	<i>Vermivora celata</i>	ocwa	2.0	2.0	0.0
White-breasted nuthatch	<i>Sitta carolinensis</i>	wbnu	2.0	1.0	0.0
Clay-coloured sparrow	<i>Spizella pallida</i>	ccsp	1.0	1.0	24.0
Northern waterthrush	<i>Seiurus noveboracensis</i>	nowa	1.0	1.5	0.0
Olive-sided flycatcher	<i>Contopus cooperi</i>	osfl	1.0	0.0	0.0
Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>	ybfl	1.0	0.0	0.0
Evening grosbeak	<i>Coccothraustes vespertinus</i>	evgr	0.5	0.0	0.0
LeConte's sparrow	<i>Ammodramus leconteii</i>	lcsp	0.0	0.0	2.0
Song sparrow	<i>Melospiza melodia</i>	sosp	0.0	0.0	23.7
White-winged crossbill	<i>Loxia leucoptera</i>	wwcr	0.0	0.5	0.0

† Includes stations allocated as reference points for clearcuts.

\* Not all coniferous forest stations were sampled in both years.