

BOREAL FOREST SONGBIRD COMMUNITIES OF THE LIARD VALLEY, NORTHWEST TERRITORIES, CANADA

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Abstract. Songbird communities in the boreal forest of the Liard Valley, Northwest Territories, Canada, are described after three years of study. Point count stations ($n = 195$) were placed in six types of forest (mature deciduous, coniferous, and mixedwood; young forests; wooded bogs; clearcuts) in a 700-km² area. Vegetation characteristics at each station were also measured. Eighty-five species of birds (59 passerine species) occurred in 11 647 detections. Mixedwood forests had the highest richness of songbirds (~41 species per 800 individuals) of the six forest types, and contained approximately 30% more individuals than nearly pure coniferous or deciduous forests. Species richness and relative abundance was 10–50% lower than in comparable forests farther south and east, and the difference was most pronounced in deciduous forests. Communities were dominated by a few species, especially Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*) and Chipping Sparrow (*Spizella passerina*). White-throated Sparrow (*Zonotrichia albicollis*), a dominant species in boreal forests farther south, was notably scarce in all forests except clearcuts. Clearcuts and wooded bogs had the simplest communities, but had unique species assemblages. Canonical correspondence analysis showed that the bird community was well correlated with vegetation structure. The primary gradient in upland forests was from deciduous to coniferous forests (also young to old, respectively). The secondary gradient was from structurally simple to complex forests. These results allow comparisons with other boreal areas to understand regional patterns and help describe the bird community for conservation purposes.

Key words: boreal forest, community, mixedwood, Northwest Territories, ordination, songbird, succession.

Comunidades de Aves Canoras de Bosques Boreales del Valle de Liard, Territorios del Noroeste, Canadá

Resumen. Luego de tres años de estudio, se describen las comunidades de aves canoras de bosques boreales del Valle de Liard, Territorios del Noroeste, Canadá. Se ubicaron estaciones de conteo de punto ($n = 195$) en seis tipos de bosque (maduro caducifolio, conífero y de maderas mixtas; bosques jóvenes; pantanos arbolados; zonas taladas) en un área de 700 km². Las características de la vegetación en cada estación también fueron medidas. Se registraron 85 especies de aves (59 especies de paserinas) en 11 647 detecciones. Los bosques mixtos presentaron la mayor riqueza de aves canoras (~41 especies por 800 individuos) de los seis tipos de bosque, y contuvieron aproximadamente 30% individuos más que los bosques de coníferas y los caducifolios. La riqueza de especies y la abundancia relativa fue 10–50% menor que en bosques comparables más al sur y al este, y la diferencia fue más pronunciada en los bosques caducifolios. Las comunidades estuvieron dominadas por unas pocas especies, especialmente *Vermivora peregrina*, *Dendroica magnolia*, *Catharus ustulatus*, *Dendroica coronata* y *Spizella passerina*. *Zonotrichia albicollis*, una especie dominante en bosques boreales más al sur, fue notablemente escasa en todos los bosques, excepto en las zonas taladas. Las áreas taladas y los pantanos arbolados tuvieron las comunidades más simples, pero presentaron ensamblajes únicos. Análisis de correspondencia canónica mostraron que la comunidad de aves estuvo bien correlacionada con la estructura de la vegetación. El gradiente primario en bosques de zonas altas fue de bosque caducifolio a conífero (también de joven a viejo, respectivamente). El gradiente secundario fue de bosques estructuralmente simples a bosques complejos. Estos resultados permiten hacer comparaciones con otros bosques boreales para entender los patrones regionales y ayudar a describir las comunidades de aves con fines de conservación.

INTRODUCTION

There is still remarkably little known about the specific habitat relationships and community structure of songbird communities in Canada's western boreal forest. Qualitative habitat relationships of most forest bird species are known across their range. However, understanding how the relative abundance of species is influenced by measured forest attributes is less well understood in the boreal forest, as is regional variation. Only in the last decade has an appreciable amount of data been collected and summarized from the southern parts of these forests (Stelfox 1995, Schmiegelow et al. 1997, Hobson and Bayne 2000a). Prior to these studies, available information often lacked detailed habitat data (Kirk et al. 1996), had few samples (Erskine 1977) or covered one or a few forest types (e.g., Westworth and Telfer 1993). There are still large areas (especially north of 60°N latitude) where basic inventories of species are incomplete, and no site-specific data are available regarding relative abundances or detailed habitat associations. Almost no areas have reliable population trend information, primarily owing to the lack of road access and the consequent lack of Breeding Bird Survey (BBS) routes. Understanding complex processes such as response to landscape fragmentation or cumulative effects of development is not possible without these basic data.

Some patterns of songbird community ecology have been identified throughout the western Canadian boreal forest. Bird communities of forests dominated by pine (*Pinus* spp.) or black spruce (*Picea mariana*) usually contain fewer species and individuals than a comparable sample of forests dominated by deciduous trees, white spruce, or a mix of the two (Hobson and Bayne 2000a). Mature forests often contain fewer bird species and individuals than older or younger forests of the same type (Schieck and Nietfeld 1995, but see Hobson and Bayne 2000b). Several species are bimodal in their occurrence across forests of different ages, usually avoiding the mature (closed canopy) age class (Schieck and Nietfeld 1995, Westworth and Telfer 1993). Forests regenerating from clearcuts often contain different species than forests regenerating from fires (Hobson and Schieck 1999). D. A. Kirk and M. Csizy (unpubl. report; available from CSM) found that, in multiple

studies across western Canada, species occurrence was closely correlated to the deciduous component of the forest (and therefore other variables correlated with the presence of deciduous trees). An improved understanding of boreal forest songbird communities is slowly emerging.

The Liard Valley in the Northwest Territories is one of the areas of the boreal forest where very little is known about the bird community. No regional studies have analyzed detailed habitat data, and other studies in the region only collected data for one year (Erskine 1977, Greenberg et al. 1999) except data from an adjacent area in the Yukon (C. Eckert et al., unpubl. data) and the Fort Liard BBS route. Machtans (2000) provided a brief regional synopsis of the bird community. The primary objective of this study was to describe the forest songbird community of the area. We compare and contrast richness and relative density of the communities within the area and region, describe the bird communities associated with the major forest types, and relate the relative abundance of species to particular habitat attributes.

METHODS

STUDY AREA

The Liard Valley is in the extreme southwest corner of the Northwest Territories, Canada, immediately north of the British Columbia border and east of the Yukon border. It is bounded by the Franklin Mountains to the west, while the area to the east quickly becomes low-relief boreal forest. This locale has relatively warm summers and winters, considering the latitude, and has high precipitation relative to other areas in the southern Northwest Territories. Annually, Fort Liard (60°15'N, 123°30'W) averages 150 frost-free days, has a mean temperature of -1.3°C and receives ~450 mm of precipitation. The mean July high and low temperatures are 23.2°C and 11.1°C respectively, and an average of 86.7 mm of rain falls in July. Annually, this is almost 2°C warmer with 30% more precipitation than nearby Fort Simpson (200 km north; Environment Canada 1982). All bird and habitat data were collected within a 10-km-wide and 70-km-long corridor that ended approximately 50 km north of Fort Liard.

Forests are generally old and tall in the area and achieve vigor similar to areas farther south because of the local climate and physiographic

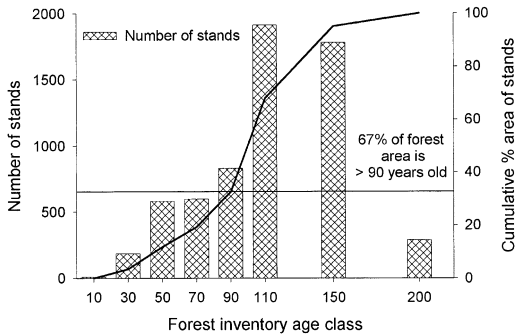


FIGURE 1. Area distribution of forest age classes in the southern part of the Liard Valley, Northwest Territories, Canada. The graph data include all forest types in a 1994 forest inventory of ~2300 km² bordering British Columbia to the south and the Yukon Territory to the west. Two-thirds of the forested area in the inventory is >90 years old.

features. In a recent forest inventory, two-thirds of the area was >90 years old (Fig. 1). In this study, trees cored ($n = 167$) in stands surveyed for birds revealed black spruce up to 272 years old, white spruce (*Picea glauca*) to 242 years, and balsam poplar (*Populus balsamifera*) up to 210 years old. We also found balsam poplar up to 115 cm dbh (diameter at breast height), trembling aspen (*Populus tremuloides*) up to 92 cm dbh, and white spruce up to 85 cm dbh. Individual trees were up to 45 m tall, while typical canopies in the older forests reached ≥ 30 m. Old (>90 years) upland, mesic stands cover 43% of the forested area. Most of those stands (79%) were 25 m or taller. Within the Liard Valley, pure stands of white spruce ($\geq 80\%$ monotypic) averaged 24 ± 36 (SD) ha in size; pure deciduous stands (aspen, poplar, and white birch [*Betula papyrifera*]) averaged 51 ± 85 ha, and mixedwood stands averaged 40 ± 61 ha in size. Extensive, continuous wetland forests (dominated by black spruce and larch [*Larix laricina*], with lesser amounts of jack pine [*Pinus banksiana*]) can cover much larger areas (stands >2000 ha). Prevalent anthropogenic disturbances include natural gas exploration and development (seismic lines, pipelines, roads, well sites) and some commercial forestry.

SURVEY METHODS

We identified five major stand types for surveys: old mesic forests (coniferous, deciduous, or mixedwood; ≥ 90 -year age class), young forests (naturally regenerating; <90-year age class), and

hygric forests (wooded bogs). There are also subalpine forests and natural dwarf-birch shrublands but these were not sampled. We considered regenerating clearcuts as a sixth type of forest in our study.

Study stands were chosen based on two criteria: that they were accessible on foot (limiting us to within ~5 km of the only road in the area) and they were large enough (>15 ha) to contain three point count stations. The stations were separated by ≥ 300 m, were ≥ 150 m from the stand edges, and were ≥ 100 m away from any other disturbances (such as seismic lines). We sampled practically all upland stands fitting these criteria near Fort Liard, and added as many stands of other forest types as resources permitted. All clearcuts were too small to meet point-count layout criteria, so points were spaced more closely and birds were counted in a 50-m radius. Stand types were determined from the existing 1994 inventory (GNWT 1994) covering part of the area, and from the 1982 inventory (INAC 1982) in areas beyond the newer maps. All were ground truthed prior to placement of points to ensure there were no major inventory classification errors. Aerial photos from 1991 and 1997 were also used for planning. Forty-three stands were sampled in 1998–2000 (all upland), and an additional 22 stands (all types) were sampled in 1999–2000. The location of each point count station was recorded with a handheld GPS unit (June 2000). Continuous stands on the inventory that were bisected by roads were considered two stands.

Point counts (three per stand) were used to sample birds, with methodological recommendations and considerations from Ralph et al. (1993, 1995), Mac Nally (1997), Dettmers et al. (1999), and Drapeau et al. (1999). Birds were identified (and, if possible, sexed) within a 50-m, a 100-m, and an unlimited radius from each permanently marked station. Behavior was noted, including vocalization type and breeding evidence. Counts lasted 10 min. Each location was visited twice per season, in early and late June, by different observers. Sampling occurred during 04:00–09:00 MST on days where wind was Beaufort 3 or less and it was not raining. All observers were experienced and were refreshed onsite for distance estimation and species identification. Observers recorded any songs or calls they did not recognize using a parabolic micro-

phone in the field. The recorded sounds were identified later by consensus of all observers.

Vegetation was sampled at each point-count station using a methodology similar to that used in Schmiegelow et al. (1997), a modification of BBIRD protocol (Martin 1997). Four 11.3-m-radius plots were surveyed at each point-count location (i.e., 195 locations \times 4 plots): one plot centered on the point count station, and three plots 70 m away at 0°, 120°, and 240°. Within each plot all trees (>8 cm dbh), poles (3–8 cm dbh), saplings (<3 cm dbh), and snags (standing dead trees) were enumerated by species and dbh. Stature of all trees was also recorded (canopy-level; dominant [\geq 5 m above canopy]; suppressed [\geq 5 m below canopy]; subcanopy). Downed woody debris (DWD; >8 cm diameter, >50 cm long) was recorded along the north-south diameter of the plot. Rot class of snags and DWD were recorded as in figure 3.1 and table 3.1, respectively of Lee, Crites, and Stelfox (1995). Cover estimates were made for major understory species or groups and each shrub species. Stems of tall shrub species (mostly *Alnus* spp. or *Salix* spp.) were counted in two pre-selected quarters of the circle. Canopy, subcanopy, and tall shrub layer height were measured in the area of the plot, and canopy cover was measured every three steps along the transects between the center plot and the three satellite plots using an ocular tube.

STATISTICAL ANALYSES

Bird data were summarized differently for various analyses. However, in all cases where data are summarized by point-count location or stand, the abundance at one point-count location was taken as the maximum of the two visits in each year (Blondel et al. 1981). Analyses are only presented from the 50-m radius. We also completed all our analyses at 100-m and unlimited sampling distances and confirmed that all reported trends existed independent of, or were not contradicted by, sample-scale issues. Using a 50-m radius allowed comparisons with all stand types (clearcuts had only 50-m-radius counts). It also alleviated the biases associated with differential detection in various habitats (Schieck 1997), and we believed the 50-m distance provided the most certainty with regard to distance estimates and identification. No experienced observers, including the authors, believed that estimating aural detection distances

beyond 50 or 60 m was accurate enough to justify the use of variable circular-plot techniques and analyses (in addition to other fundamental violations of assumptions for that technique). No raptors or waterbirds were included in analyses.

Species richness and individual accumulation rates were calculated using EstimateS 5.0.1 software (Colwell 1997). Each detection was weighted equally (i.e., abundance = 1 for each individual detection), regardless of bird behavior (singing, calling, etc.) except flyovers, which were deleted. Both predicted and observed species richness were calculated, the former using the Incidence-based Coverage Estimator (Lee and Chao 1994, Chazdon et al. 1998), the latter using rarefaction curves of observed species (“Sobs” in the software). Each visit to each location in each stand and year was considered a measurement or sample of the species richness of a forest type; therefore $n = 1036$ for this analysis.

Cluster analysis (using TWINSpan) was used to group stands into biologically derived habitat classes. Each bird observation was weighted by behavior: singing males = 1, pairs and nests = 2, calls and visual contact only = 0.5, and flyovers = 0 (Schmiegelow et al. 1997). This weighting was the only way (with our data) we could increase our confidence that we were using territorial individuals to elucidate habitat associations. The abundance of each species in each stand was calculated by averaging all years and points within that stand, then converting that to a relative abundance for each stand (i.e., total abundance of all species in a stand is 100%; Hobson and Bayne 2000a). All TWINSpan defaults were used. Once TWINSpan had classified the bird communities, we reassigned habitat names to the classes based on the predominant forest type in each group.

Ordinations of the upland forest bird community and vegetation characteristics were performed in CANOCO 4 (ter Braak and Šmilauer 1998). CANOCO options were set to “down weighting of rare species” and “interspecies distances and biplot scaling.” Input data were treated as in the TWINSpan analyses. Other analyses were performed in SPSS 8.0 (SPSS 1998) unless otherwise noted. An effort was made to avoid presenting uninformative statistical tests (Johnson 1999, Anderson et al. 2001).

Species were included in analyses as follows: Including all behaviors, there were 60 species of

passerines and woodpeckers observed within 50 m (used in richness analyses). Two species were flyovers, 11 were rare (present at <3 stands), and Common Raven (*Corvus corax*) was excluded since they roam over large areas. Therefore, 46 species were available for TWINSpan analyses. Since only coniferous, deciduous, and mixedwood forests were used in ordinations, a further seven “rare” species were excluded from this reduced dataset. Thirty-nine species remained for ordination. A table available from the authors indicates which species were used in each analysis.

Vegetation data were summarized by calculating per-ha values on sums of counts for each stand, or means for other data. Typically, 0.48 ha (3 point-count locations \times 4 plots per location \times 0.04 ha per plot) was surveyed in each stand. Volume of DWD was calculated using the formula $v = (\pi^2/8l)\Sigma(n,d_i^2)$, from Van Wagner (1968), where v is the volume per unit area, l is the total transect length, and n is the number of pieces of diameter d (m). For this study, $n = 1$ since individual pieces were enumerated and $l = 271.2$ m (twelve 22.6-m transects per stand). Volume per ha is then calculated as volume per unit area (m) \times 10 000 m² ha⁻¹ (m³ ha⁻¹; matching calculations in table 4.4 of Lee, Crites, et al. 1995).

Differences in vegetation among habitats was assessed with one-way ANOVA, but significance was assessed using *post-hoc* tests appropriate to homoscedasticity restrictions; least significance difference (LSD) was used for groups with similar between-site variance, while the Dunnett T3 was used for violations of homoscedasticity. Values reported are means \pm SD.

RESULTS

HABITAT

Birds grouped the upland forests into communities different than those defined by forest inventory maps or detailed vegetation data. The *a priori* study design considered pure stands to have $\geq 80\%$ deciduous or coniferous cover, while the remainder were classified as mixedwood (column 1, Table 1; similar to Hobson and Bayne 2000a). Based on detailed counts of canopy or dominant trees in the surveyed stands, the upland forest totals were revised (column 2, Table 1). TWINSpan arrangement of the forest stands resulted in a different classification of for-

TABLE 1. Number of forest stands in a classification derived from three methods: aerial-photo interpretation (forest inventory data); detailed vegetation surveys in the inventory stands, but around bird plots; and bird-driven classifications. The bird-driven classification was derived from TWINSpan classification of the habitat data using bird observations. For the first two classes, coniferous and deciduous forests stands contained $\geq 80\%$ coniferous or deciduous content; intermediate stands were classified as mixedwood. While bird communities are clearly tied to broad habitat classes, the bird-driven habitat classification is somewhat different from arbitrary, human-picked classes of mature forest types.

Stand type	Forest inventory data	Vegetation survey data	Bird-driven class
Deciduous	12	8	14
Mixedwood	21	26	13
Coniferous	15	14	24
Young (<90 years old)	6	6	3
Wooded bog	5	5	5
Clearcut	—	6	6

est type, based on associations in the bird communities. TWINSpan broke the groups as follows: wooded bogs and clearcuts were first separated from all other forest (2 groups). Wooded bogs and clearcuts were then separated, as were young (<90 years) and deciduous forests from mixed and coniferous forests (4 groups). The third level of TWINSpan separated the forests into the classes in column 3, Table 1 (6 groups). An additional level of division occurred within both the wooded bogs and clearcuts (an artifact of using 4 stands as the stopping rule in TWINSpan), but it was not biologically relevant, so six groups are presented rather than the eight present at the third TWINSpan division. This biologically derived classification was used for subsequent summaries of the vegetation and bird communities.

Structural attributes of the forests are summarized in Table 2 (inventory data) and in Table 3 (detailed site-specific data) for comparison. The large differences between the six major types of forest made statistical tests uninformative, so tests were only performed on the three classes of older upland forest (Table 3). Deciduous forests were dominated by aspen, with typically <10% of the canopy composed of conifers. Deciduous forests tended to be younger, with denser canopies and smaller diameter deciduous trees than the other two mature upland

TABLE 2. Mean values (range) of forest stand vegetation variables from forest inventory maps for the habitat groups identified by classification of the bird community in the Liard Valley, Northwest Territories, Canada. Age classes are as in Figure 1. The inventory data provide height in 5-m classes, and % dominant trees in 10% classes. For this table, deciduous = trembling aspen, balsam poplar, and white birch; coniferous = white spruce, except for wooded bog where it is black spruce.

Habitat	Forest inventory vegetation ranges			
	Age	Canopy height	% Deciduous	% Coniferous
Deciduous	104 (50–150)	23 (10–30)	90 (30–100)	10 (0–70)
Mixedwood	124 (110–150)	29 (25–35)	62 (40–90)	38 (10–60)
Coniferous	132 (90–150)	26 (20–30)	22 (0–70)	78 (30–100)
Young	50 (50)	12 (5–15)	60 (20–80)	40 (20–80)
Wooded bog	74 (50–90)	8 (5–10)	0 (0)	72 (60–80) ^b
Clearcut ^a	—	—	—	—

^a Clearcuts were not included on the inventory.

^b Remainder of cover is from larch and jack pine.

stand types (Table 3). Deciduous forests also tended to have denser subcanopies and fewer deciduous saplings and poles than coniferous or mixedwood forests. Many deciduous stands had vigorous growth of young white spruce that indicated the stands would later become conifer dominated. They had less downed woody material, as would be expected from their ages. Mixedwood forests were nearly an even mix of conifers and deciduous trees and tended to have the tallest canopies. Coniferous forests tended to be the oldest forests, and typically had <25% deciduous canopy trees. Some stands were nearly monotypic; two stands in a large (243 ha) floodplain spruce forest had a single deciduous canopy tree noted from 24 vegetation plots. Along with mixedwood forests, coniferous forests had significantly more DWD than deciduous forests, and had higher densities of deciduous saplings and poles in their understory.

The average values for canopy tree prevalence in habitat groups identified by the birds agreed reasonably well with the *a priori* study design. Eighty-nine percent of canopy trees were deciduous (95% CI: 81–97, range 54–100) in the “deciduous” group. Forty-three percent of canopy trees were deciduous (95% CI: 34–51, range 18–75) in the “mixedwood” group. Twenty percent of the canopy trees were deciduous (95% CI: 14–26, range 0–50) in the “coniferous” group.

BIRD COMMUNITY OVERVIEW

We detected 4303 individuals within 50 m of 1037 point-count surveys at 195 locations in three years (11 647 individuals without a distance limit). Fifty-one species were passerines

and another seven were woodpeckers. The remainder were raptors or waterbirds, except Ruffed Grouse (*Bonasa umbellus*) and Common Nighthawk (*Chordeiles minor*). The five most common species made up almost half of all detections (of the 60 species noted above). They were Tennessee Warbler (*Vermivora peregrina*; 12%), Magnolia Warbler (*Dendroica magnolia*; 12%), Swainson’s Thrush (*Catharus ustulatus*; 8%), Yellow-rumped Warbler (*Dendroica coronata*; 7%) and Chipping Sparrow (*Spizella passerina*; 6%). These totals are biased since all forest types were not sampled equally. A table is available from the authors that provides mean counts \pm SD by species for 50-m counts.

There was a high degree of overlap in the dominant bird species in mixedwood and coniferous forests, and, to a lesser extent, in deciduous and young forests (Table 4). Both wooded bogs and clearcuts had more distinctive assemblages, either dominated by species that preferred open, shrubby habitats or by habitat specialists. White-throated Sparrows (*Zonotrichia albicollis*) were notably scarce in the upland communities, while Magnolia Warblers were unusually common.

Few species were true habitat specialists. Specialists were defined by being restricted to one stand type (of the habitat groups defined by the bird community). Only the Palm Warbler (*Dendroica palmarum*; wooded bogs) and the Black-backed Woodpecker (*Picoides arcticus*; coniferous forests) were found exclusively in their respective stand types. Four other species were essentially specialists, each occurring in only a single stand outside of their usual stand type:

TABLE 3. Summary statistics for vegetation data collected within each habitat where birds were surveyed in the Liard Valley, Northwest Territories, Canada. Values presented as means \pm SD. Habitat groups were determined by TWINSpan classification based on bird communities (see Table 1). Measurements are based on 12 vegetation plots per stand. Values for the first three stand types are statistically different ($P < 0.01$ except $P_{\text{canopy ht}} < 0.03$) if they do not share the same lowercase letter.

Variable (units)	Stand type (<i>n</i>)					
	Deciduous (14)	Mixedwood (13)	Coniferous (24)	Young (3)	Wooded bog (5)	Clearcuts (6)
Canopy structure						
Age ^a (<i>n</i>)	109.0 \pm 34.2 (10) a	167.8 \pm 15.5 (10) b	178.9 \pm 30.0 (17) b	50.0 \pm 1.1 (2)	55.3 \pm 2.9 (3)	3.7 \pm 2.1 (6)
Canopy height (m)	30.6 \pm 3.4 a	32.4 \pm 1.9 b	29.7 \pm 2.9 a	13.5 \pm 5.6	7.5 \pm 1.6	—
Canopy cover (%)	68 \pm 8 a	61 \pm 12 ab	55 \pm 12 b	57 \pm 15	7 \pm 2	4 \pm 6
No. canopy trees per ha	450 \pm 141	413 \pm 128	379 \pm 114	455 \pm 328	269 \pm 125	7 \pm 16
No. canopy deciduous trees per ha	411 \pm 167 a	180 \pm 51 b	77 \pm 60 c	381 \pm 313	12 \pm 15	6 \pm 13
Canopy deciduous average dbh (cm)	27.1 \pm 7.1 a	34.6 \pm 3.5 b	34.7 \pm 6.4 b	12.1 \pm 3.1	12.7 \pm 2.9	59.1 \pm 39.5
No. canopy coniferous trees per ha	39 \pm 45 a	233 \pm 108 b	302 \pm 102 b	74 \pm 38	257 \pm 123	1 \pm 3
Canopy coniferous average dbh (cm)	28.5 \pm 6.3	29.3 \pm 3.0	30.1 \pm 3.8	10.3 \pm 1.1	9.8 \pm 0.7	30.8 \pm 0
Subcanopy and tall shrub layers						
No. subcanopy trees per ha	362 \pm 200 a	187 \pm 39 b	230 \pm 76 ab	166 \pm 160	4 \pm 9	40 \pm 38
No. deciduous saplings and poles per ha ^b	219 \pm 199 a	516 \pm 260 b	600 \pm 445 b	948 \pm 645	91 \pm 184	1409 \pm 803
No. coniferous saplings and poles per ha	228 \pm 279	45 \pm 27	61 \pm 44	5943 \pm 2396	3763 \pm 745	50 \pm 77
No. alder stems per ha	3419 \pm 1720	3286 \pm 2399	3198 \pm 2263	1260 \pm 810	521 \pm 446	1031 \pm 1076
Snags and downed woody debris (DWD)						
Median DWD rot class ^c	3	4	3	7	5	4
DWD volume (m ³ ha ⁻¹) ^d	75.8 \pm 44.7 a	156.1 \pm 49.9 b	157.4 \pm 54.1 b	87.8 \pm 10.7	12.0 \pm 9.4	174.2 \pm 165.2
No. snags per ha	156.3 \pm 80.2	146.5 \pm 60.9	146.4 \pm 43.8	21.5 \pm 24.3	17.1 \pm 7.7	11.1 \pm 12.3
Mean snag dbh (cm)	18.3 \pm 6.0 a	24.5 \pm 3.9 b	22.4 \pm 3.0 ab	16.9 \pm 1.8	9.7 \pm 1.0	21.0 \pm 8.7
Mean snag height (m)	10.5 \pm 2.1	10.0 \pm 2.8	10.4 \pm 2.2	3.3 \pm 1.7	4.8 \pm 0.3	5.3 \pm 2.0
Median snag decay class	5	2	2	2	3	5

^a The number of stands where tree core data were used to calculate the mean. The mean was not different (paired *t*-test, $P = 0.08$) when inventory ages were substituted for missing values in the tree core dataset.

^b Saplings and poles are trees smaller than 8 cm dbh and >2 m tall.

^c Rot classes (1–7) pertain to table 3.1 of Lee, Crites, and Stelfox (1995). 1 = recent downed wood; 7 = DWD that is nearly 100% humified.

^d Counting all pieces >8 cm diameter and >50 cm long.

TABLE 4. Differences in the rank abundance of the most common species in each of the six habitats surveyed in the Liard Valley, Northwest Territories, Canada. Data are summarized from 50-m-radius point counts as grouped by the TWINSpan analysis. The ranks are based on total detections uncorrected for behavior (singing, calling, etc.), excluding flyovers. Scientific names of species in the table are found in the text.^a Nine additional species were observed within 50 m and used in analyses, but did not rank in the 15 most common species in any habitat.^b

Species	Rank abundance of species					
	Coniferous	Mixedwood	Deciduous	Young	Wooded bog	Clearcut ^c
Tennessee Warbler (TEWA)	1	2	6	3	3	4
Magnolia Warbler (MAGW)	2	1	2	5	9	6
Swainson's Thrush (SWTH)	3	6	3	2	8	
Yellow-rumped Warbler (YRWA)	4	5	7	11		
Chipping Sparrow (CHSP)	5	7	14	12	2	7
Western Tanager (WETA)	6	4				
Bay-breasted Warbler (BBWA)	7	3	13	8		
Red-breasted Nuthatch (RBNU)	8	11				
Gray Jay (GRJA)	9			13	6	
Yellow-bellied Sapsucker (YBSA)	10	9	11			
White-winged Crossbill (WWCR)	11					
Cape May Warbler (CMWA)	12					
Boreal Chickadee (BOCH)	13			15		
White-throated Sparrow (WTSP)	14				7	1
Ovenbird (OVEN)	15	8	1	9		
American Redstart (AMRE)		10	4	1		
Canada Warbler (CAWA)		12	8			
American Robin (AMRO)		13			13	10
Red-eyed Vireo (REVI)		14	5	6		
Black-and-white Warbler (BAWW)		15	12	4		
Least Flycatcher (LEFL)			9	14		9
Warbling Vireo (WAVI)			10			8
Rose-breasted Grosbeak (RBGR)			15			
Yellow-bellied Flycatcher (YBFL)				7	10	
Fox Sparrow (FOSP)				10	11	
Palm Warbler (PAWA)					1	
Hermit Thrush (HETH)					4	
Dark-eyed Junco (DEJU)					5	11
Lincoln's Sparrow (LISP)					12	5
Ruby-crowned Kinglet (RCKI)					14	
Alder Flycatcher (ALFL)					15	2
Mourning Warbler (MOWA)						3

^a Except for Warbling Vireo (*Vireo gilvus*), Red-breasted Nuthatch (*Sitta canadensis*), American Robin (*Turdus migratorius*), Cape May Warbler (*Dendroica tigrina*), Gray Jay (*Perisoreus canadensis*), Lincoln's Sparrow (*Melospiza lincolni*).

^b Other species observed and used in analyses: Downy Woodpecker (*Picoides pubescens*; DOWO), Hairy Woodpecker (*Picoides villosus*; HAWO), Northern Flicker (*Colaptes auratus*; NOFL), Pileated Woodpecker (*Dryocopus pileatus*; PIWO), Hammond's Flycatcher (*Empidonax hammondi*; HAFL), Eastern Phoebe (*Sayornis phoebe*; EAPH), Bohemian Waxwing (*Bombycilla garrulus*; BOWA), Blackpoll Warbler (*Dendroica striata*), Pine Siskin (*Carduelis pinus*; PISI).

^c Only species with more than one detection in clearcuts are listed.

Mourning Warbler (*Oporornis philadelphia*; clearcuts), Hermit Thrush (*Catharus guttatus*; wooded bogs), Golden-crowned Kinglet (*Regulus satrapa*; coniferous forests) and Three-toed Woodpecker (*Picoides tridactylus*; coniferous forests). All other species occurred in several stand types.

SPECIES RICHNESS AND ABUNDANCE

The number of species detected in a count-based study is usually incomplete (Nichols et al. 1998). Mathematical estimates of the true number of species in a community can be derived from the observed number and frequency of occurrence, relying especially on the occurrence of

rare species for the calculation. EstimateS computes several metrics, including the commonly used jackknife method (Burnham and Overton 1979) and newer, potentially more robust metrics including the Incidence-based Coverage Estimator (Lee and Chao 1994). The reliance on rare species to predict richness means that tiny errors in data collection can alter results substantially. For illustration, in 348 counts that we conducted in coniferous forests, the total predicted number of species in the community was 61. Of >2000 observations, two species were each noted once, and both were far from the observer. If they were removed from the dataset, the predicted richness would drop to 56 (9% difference). The results and interpretation could change significantly if these observations were either identification errors or distance estimation errors (i.e., if the birds were actually beyond the detection radius cutoff). This reinforced our decision to use the 50-m data and to present a simple (but negatively biased) rarefaction estimate. The choice between estimators is still unresolved (Hellmann and Fowler 1999).

Mixedwood and coniferous forests had similar observed species richness (Fig. 2a), and were the most species-rich habitats in this study. Approximately 41 species were present in samples of 800 detections. Mixedwoods were predicted to have a greater richness, (10% greater, Fig. 2b) perhaps emphasizing that the slight divergence of the coniferous and mixedwood observed species curves would continue with additional observations.

Species overlap between the mixedwoods and coniferous forests was high. Thirty-nine species were found in both habitats. Purple Finch (*Carpodacus purpureus*), Northern Waterthrush (*Seiurus noveboracensis*), Ruffed Grouse, and Western Wood-Pewee (*Contopus sordidulus*) appeared only in the mixedwood sample. Alder Flycatcher (*Empidonax alnorum*), Black-backed Woodpecker, Mourning Warbler, Orange-crowned Warbler (*Vermivora celata*), Philadelphia Vireo (*Vireo philadelphicus*), Townsend's Warbler (*Dendroica townsendi*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), and Winter Wren (*Troglodytes troglodytes*) occurred only in the coniferous sample. Most of these unique species were represented by only one or two observations in total, and it is more appropriate to consider them as chance occurrences rather than habitat specialists.

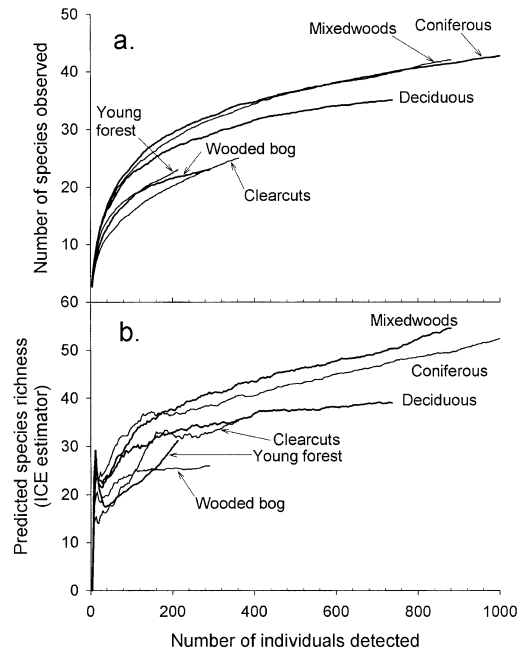


FIGURE 2. Species richness curves for songbirds in habitats in the Liard Valley, Northwest Territories, Canada. All data are from 50-m-radius point counts. (a) Rarefaction estimate of species richness (resampled observed richness); (b) prediction of species richness based on the Incidence-based Convergence Estimator (ICE; see text). Mixedwoods and coniferous forests had similar species richness, higher than other forests in the study area. Mixedwood forest was predicted to have greater species richness (b), perhaps emphasizing the slight divergence of the curves from those in (a).

Deciduous forests had many fewer species than other mature, upland forest types. It did not matter if observed or predicted values were considered. At the largest comparable sample size, deciduous forests had 14% fewer observed species (23% and 28% fewer predicted) than both coniferous and mixedwood forests (Fig. 2). Of the remaining forest types, clearcuts were predicted to have a similar number of species as deciduous forests, in contrast to the consistently lower number of actual species observed (Fig. 2a). This is a result of several observations of a single individual of a species in the clearcuts, an outcome of the heterogeneous nature of cover left from harvesting. Young forests, wooded bogs, and clearcuts all had many fewer species observed than older, upland forests. Wooded bogs had the fewest species of any forested habitat. The flattening of the predictive curve in Fig-

TABLE 5. Linear regression coefficients for a rarefaction curve of the number of individuals accumulated per 50-m point count. The regression was forced through the origin so that at zero sites there were zero individuals; therefore no y-intercepts are provided. None of the 99% confidence intervals for the slopes overlap, so all slopes are considered statistically different.

Stand type	Regression coefficient	99% CI	Estimated number in 200 counts
Mixedwood	3.96	3.96–3.96	792
Young forest	3.64	3.63–3.65	727
Coniferous	3.41	3.41–3.41	681
Deciduous	3.15	3.15–3.16	631
Wooded bogs	2.75	2.74–2.76	550
Clearcuts	2.29	2.29–2.29	458

ure 2b indicates that few new species will likely be found with additional sampling.

More birds were found in mixedwoods than in any other stand type (Table 5). The accumulation rates for number of individuals detected in each stand type showed that mixedwood forests had 9% more individuals per sample than the next habitat (young forest), and had 16% and 26% more individuals per sample than coniferous and deciduous forest respectively. Plotting the total species abundance as a function of percentage of deciduous canopy trees in the sample area (Fig. 3) made this relationship readily apparent. The quadratic relationship matched the pattern of the data well ($r^2 = 0.42$, $F_{2,47} = 17.3$, $P < 0.001$, average abundance per station was $4.56 + 0.103x - 0.001x^2$), differing only slightly from a locally weighted regression curve. A derivation where each observation was weighted equally (i.e., actual detections not based on behavior), yielded the same strong pattern ($r^2 = 0.45$, $F_{2,47} = 19.3$, $P < 0.001$, average detections per station = $5.67 + 0.106x - 0.001x^2$).

Evenness of the bird communities was assessed with rank-abundance plots. Mature forests differed little in their evenness (95% CI of slopes: coniferous, -0.056 to -0.054 ; mixedwoods, -0.06 to -0.056 ; deciduous, -0.065 to -0.06). Evenness of young forests was intermediate (95% CI of slope: -0.074 to -0.062). However, bird communities in clearcuts were dominated by a few species. The community evenness was significantly less in clearcuts and wooded bogs when compared to other forest types in the area (95% CI of slopes: clearcuts,

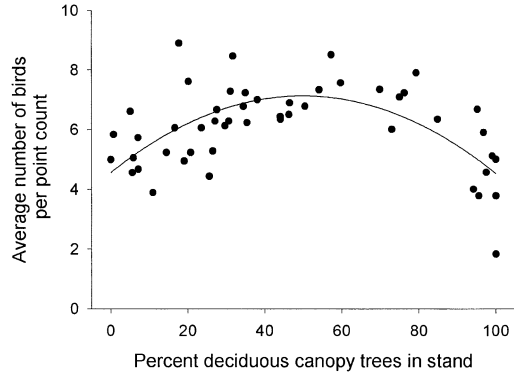


FIGURE 3. Mixedwood forests in the Liard Valley clearly supported more individuals than more monotypic forests. These data represent the average number of birds counted during one 50-m-radius point count in a stand with a given deciduous canopy percentage. Abundance is weighted by behavior (see Methods).

-0.12 to -0.11 ; wooded bogs, -0.08 to -0.075). Coupled with the low relative abundance of birds in clearcuts, these habitats therefore have the simplest bird communities in the study area.

BIRD-HABITAT RELATIONSHIPS

A DCA (detrended correspondence analysis) showed how stands were organized based on bird species associations and provided explanatory statistics to compare with a constrained ordination. As is typical with most species data sets, the percent of variation explained by the DCA is not high (Table 6). The gradient length of 2.69 (in units of standard deviations of species turnover) did not indicate a very strong unimodal response within this restricted subset of data. A value ≥ 4 would indicate species with strong habitat affinities and is the typical width of a classic Gaussian response curve (ter Braak and Šmilauer 1998). As a general rule, if sites were plotted on the ordination diagram, those separated by approximately 4 SD units would have no species in common (ter Braak 1995).

The DCA organized the sites into discrete deciduous, mixedwood, and coniferous groups that agreed well with the TWINSpan classification. Each stand was marked by its TWINSpan group, and bivariate ellipses (67% or 1 SD around each group mean) were plotted for each forest type along the two primary axes of the DCA. This resulted in a graphical representation of the coniferous-deciduous gradient identified

TABLE 6. Ordination statistics for upland bird communities in the Liard Valley, Northwest Territories, Canada. The CCA explained nearly as much species variation as the DCA, indicating that the vegetation variables describe the variation in the bird community well (or are highly correlated with variables that do). Additional statistics: the LC/WA correlation = 0.96 for the first axis of the CCA, so we used LC scores in this analysis (McCune 1997). Total inertia was 1.21; CCA sum of canonical eigenvalues was 0.65.

	Axis 1	Axis 2	Axis 3	Axis 4
Detrended Correspondence Analysis				
Eigenvalues	0.32	0.08	0.06	0.04
Gradient length (SD)	2.69	1.56	1.08	0.99
Cumulative species variance explained (%)	26	33	37	41
Canonical Correspondence Analysis				
Eigenvalues	0.29	0.10	0.06	0.04
Cumulative species variance explained (%)	24	33	38	41
Cumulative species-environment relation (%)	45	61	70	76
Monte-Carlo <i>P</i> -value of axis significance	<0.01	<0.01	<0.01	0.12

in the TWINSPLAN analysis. The mean location of each group (forest type) along the *x*-axis was significantly different (one way ANOVA, $F_{2,48} = 140.2$, $P < 0.01$, LSD, all $P < 0.01$); that is, coniferous, mixedwood, and deciduous forests have distinct bird communities. However, there was no difference in the group means along the second axis ($F_{2,48} = 0.2$, $P = 0.83$) indicating that stand type is not correlated with that axis.

The CCA (canonical correspondence analysis) explained as much species variance as an unconstrained analysis, indicating that vegetation variables represented the gradient in the species very well or are very highly correlated with the true gradient (Table 6). The first three axes of the CCA were statistically significant, but only the first two were interpreted biologically.

The CCA biplot (Fig. 4) combines information about the bird community and habitat variables of mature, mesic forests. The axes are scaled such that the correlation of each environmental variable with an axis can be read directly by drawing a perpendicular line from the axis of interest to the head of the arrow. Therefore, longer arrows are more correlated with the data than shorter arrows. Horizontal or vertical arrows are highly correlated with only one axis, while more diagonal arrows are correlated with both axes. The scores of the species on the axes are arbitrary, as they have been rescaled to fit into the diagram (scaled at 0.5). However, their relative position to other species and from the axes is indicative of their response to those axes. Species near the center of the diagram would likely be most common in mixedwood forests, while species farther from the origin would be

more abundant in more monotypic forests. Species such as Least Flycatcher (*Empidonax minimus*) or Fox Sparrow (*Passerella iliaca*) increased in abundance as the percent deciduous canopy increased, versus species such as Magnolia Warbler, Bay-breasted Warbler (*Dendroica castanea*), and Yellow-rumped Warbler that reached peak abundances when values of coniferous and deciduous trees were intermediate (i.e., mixedwood). Generalists would also appear in the center of the diagram, so interpretation must be aided by the log-linear responses of the species to the ordination axis (not presented here). Two examples are Swainson's Thrush and Yellow-bellied Sapsucker (*Sphyrapicus varius*), two species that did not have a unimodal response to the first axis.

Nearly all vegetation variables were included in the CCA diagram to prevent overly subjective inclusion by either the investigator or from forward selection of variables. Within the resulting analysis, the highest inflation factor (a measure of how correlated variables are) for the environmental variables was 6.35, well below the recommended maximum of 20 (which would indicate a near-perfect correlation with other variables, ter Braak and Šmilauer 1998). The only variables excluded were the measures of rot of snags and DWD (the only categorical variables) and the number of canopy trees per ha. The latter is equal to the sum of deciduous and coniferous tree density, which were used in the analysis.

The CCA showed a distinct gradient from coniferous to deciduous forests along the first axis, collinear with an old-to-young age spread, re-

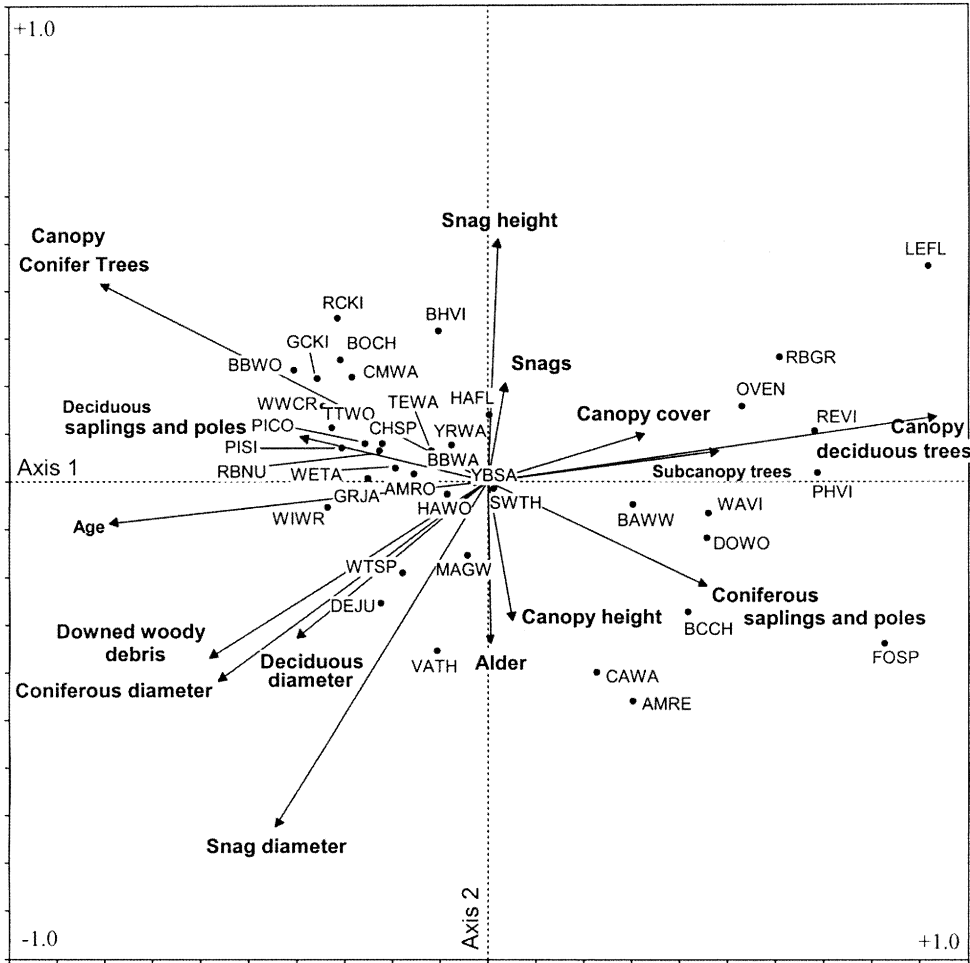


FIGURE 4. Canonical correspondence analysis of bird-habitat relationships for upland forests >90 years of age in Liard Valley, Northwest Territories, Canada. The perpendicular line from each axis to the arrowhead of an environmental variable is the correlation of that variable with that axis. Therefore, longer arrows are more important to the gradient than shorter arrows. Bird scores are scaled at 0.5 from their ordination scores in CANOCO. Both axes are statistically significant at $P < 0.01$. The primary gradient is from coniferous to deciduous forests (left to right) and from structurally simple forests to complex (top to bottom). Species nearer the center had intermediate correlations with the environmental variables (more ubiquitous), contrasting with species far from the center that were strongly correlated with habitat variables (more defined habitat requirements). Four-letter codes for birds are in Table 4, except BHVI (Blue-headed Vireo), GCKI (Golden-crowned Kinglet), WIWR (Winter Wren), VATH (Varied Thrush), BCCH (Black-capped Chickadee), PHVI (Philadelphia Vireo), BBWO (Black-backed Woodpecker), TTWO (Three-toed Woodpecker), PICO (*Picoides* spp.).

spectively. Using the biplot interpretation rule, Least Flycatcher, Fox Sparrow, Red-eyed Vireo (*Vireo olivaceus*), Philadelphia Vireo, Rose-breasted Grosbeak (*Peuceptes ludovicianus*), and Ovenbird (*Seiurus aurocapillus*) had higher abundance with increasing density of deciduous trees in the canopy, and a strong response relative to other species. Conversely, species such as Black-backed Woodpecker, Golden-crowned

Kinglet, White-winged Crossbill (*Loxia leucoptera*), Winter Wren, and Three-toed Woodpecker increased in abundance with increasing numbers of canopy conifer trees. The age variable highlights that the general succession pattern follows a typical deciduous-to-coniferous trajectory. Many species did have a unimodal response (i.e., statistically identifiable habitat preferences) to the main gradient in the ordination analysis

presented below, but for brevity, detailed information is not presented here.

The second axis of the CCA is highly (negatively) correlated with increasing snag diameter (top to bottom of graph), along with increasingly large average tree sizes and amount of coarse woody debris (Fig. 4). It was moderately positively correlated with increasing snag height and increasing density of canopy conifers. Our biological generalization of these variables is an increasingly complex forest structure from top to bottom of the ordination diagram. This correlates well with increased alder in the understory, and fewer snags (assuming many smaller snags are indicative of canopy thinning). Additionally, increasing amounts of coarse woody debris was correlated with increased size of DWD, indicative of canopy break-up and larger downed trees. Species that responded to this gradient included Least Flycatcher, Blue-headed Vireo (*Vireo solitarius*), Boreal Chickadee (*Poecile hudsonica*), Ruby-crowned Kinglet (*Regulus calendula*), and Rose breasted Grosbeak, which occupied simpler forests; and American Redstart (*Setophaga ruticilla*), Canada Warbler (*Wilsonia canadensis*), Varied Thrush (*Ixoreus naevius*), Black-capped Chickadee (*Poecile atricapilla*), Dark-eyed Junco (*Junco hyemalis*), and White-throated Sparrow, which responded to more complex forest structure. Some of these species are uncommon in these forest types, so contact the authors for the table with relative abundance before drawing conclusions from these relationships. For instance, White-throated Sparrows were 10 times more abundant in clearcuts than in any of the forest types represented in Figure 4. Similarly, certain species such as Fox Sparrow, American Redstart and Black-and-white Warbler (*Mniotilta varia*) also showed high abundance in younger forests (a bimodal response to forest age), so their habitat preferences are not completely captured by this analysis.

DISCUSSION

BIRD COMMUNITY

The Liard Valley is far enough north and west that songbird communities are simpler than in other areas of boreal mixedwood forest. The vast majority of all individuals encountered were from the 10 most common species. In the Liard Valley, the five most common species comprised 50–77% (value dependent on sampling radius)

of all birds detected, and the 10 most common comprised 79–95% of birds detected in any one of the six stand types (Table 4). The heavy weighting of the community to a few species occurs in other areas of the boreal forest. However, as species richness drops to the west and north, a few species become numerically very dominant in the community. In Alberta, Schmiegelow et al. (1997) reported 52% and 73% for the top five and 10 respectively (their appendix) from a species list that is very similar to the Liard Valley. In Saskatchewan, Hobson and Bayne (2000a) reported 42% and 63% from a community that is more species rich and even. These recent, extensive studies allow us to better quantify how the density of birds drops across the boreal region from east to west and north, noted earlier by Erskine (1977).

The most significant difference in the songbird communities in the Liard Valley, when compared to areas farther south and east, concerns two species that dominate the respective bird communities. White-throated Sparrow is one of the most common species in upland forests in the western boreal forest (Schieck and Nietfeld 1995 [second most common], Schmiegelow et al. 1997 [most common], Hobson and Bayne 2000a [sixth most common]). However, very few White-throated Sparrows are found in upland forest in the Liard Valley, yet they are common in clearcuts (Table 4). Conversely, the Magnolia Warbler was very common in upland forests in the Liard Valley (Table 4), and was found in all other habitats. In contrast, the species was almost absent from both Alberta studies (Schieck and Nietfeld 1995, Schmiegelow et al. 1997), and in Saskatchewan the species was ranked fifteenth in upland forests (Hobson and Bayne 2000a).

The reasons for these patterns are not clear from our level of analysis. The decline in abundance of White-throated Sparrows in the north and west of its range was documented by Erskine (1977). No ecological explanation was given. However, he noted they were still very abundant in disturbed areas in that edge of their range, similar to results from this study (clearcuts) and the local BBS route. We cannot offer a convincing explanation except to speculate that the species is simply lower in abundance at the edge of its range (Brown 1984, Wiens 1989) except in ideal habitat. Magnolia Warbler is a species closely tied to coniferous trees (sum-

TABLE 7. A comparison of community richness and abundance measures in boreal forests in Saskatchewan and the Northwest Territories (NWT), Canada. Saskatchewan forests (Hobson and Bayne 2001a) had higher species richness and numbers of individuals detected in all comparable upland forest types, with the largest difference in pure deciduous forests. Data are from unlimited radius, 10-min point counts (differing from other data presented in this manuscript). Data in each category were used from the study with smaller sample size, and data were drawn randomly from the study with the larger sample size until the two were equal. Richness is calculated from equal numbers of individuals in a given sample, while relative abundance is compared with an equal number of counts. All values are means (\pm SD when not all data were used) from the EstimateS software. Differences reflect the greater richness and relative abundance in the Saskatchewan samples.

	Observed number of species	Predicted number of species	Richness difference b/w studies	Observed number of individuals	Individuals difference b/w studies
Mixedwoods ($n = 3511$ individuals)				($n = 286$ counts)	
Saskatchewan	62 ± 2	68 ± 5		3881 ± 65	
NWT	53	57	+17%	3499 ± 4	+11%
Deciduous ($n = 2446$ individuals)				($n = 245$ counts)	
Saskatchewan	66 ± 1	73 ± 3		2931 ± 10	
NWT	44	49	+50%	2436 ± 4	+20%
Coniferous ($n = 2010$ individuals)				($n = 158$ counts)	
Saskatchewan	56	64		1997 ± 5	
NWT	50 ± 2	58 ± 5	+12%	1574 ± 30	+27%

marized in Hall 1994). That alone does not account for the difference between this study and the Alberta and Saskatchewan studies. Both other studies include either conifer habitats or similar amounts of conifer understory in the other forests. Although the stands in Schmiegelow et al. (1997) are deciduous dominated, other studies from the same area that surveyed stands with more conifers still reported comparatively low numbers of the warbler (Norton and Hannon 1997, Norton et al. 2000). All BBS routes from Saskatchewan and Alberta show relatively few Magnolia Warblers (Sauer et al. 2001), as does other work from northeastern Alberta (Francis and Lumbis 1980). There is currently an outbreak of spruce budworm (*Choristoneura fumiferana*) in the Liard Valley, but the species does not usually respond to outbreaks or responds negatively (Patten and Burger 1998). Finding these large shifts in species abundance across their range is an important contribution of studies to regional modeling of bird-habitat relationships.

SPECIES RICHNESS AND ABUNDANCE

Mixedwoods were the most species-rich forest type in the study area. Coniferous forest had nearly as many species, but mixedwood forests had many more individuals. Compared to nearly pure coniferous or deciduous forests (90% monotypic), mixedwood forests had approxi-

mately 30% more individuals (Fig. 3). The disproportionately high value of mixedwood forests to songbirds has been discussed by several authors, most recently in detail by Hobson and Bayne (2000a). The general conclusion is that the increased structural and floristic diversity of a mixedwood forest accounts for the differences (by increasing nest sites, foraging areas, etc.). As Hobson and Bayne (2000a) stress, replacement of mixedwoods in the boreal forest by monotypic stands following harvest is a serious concern for bird conservation. Efforts must be made to move to a mixedwood management strategy; Grover and Greenway (1999) describe economic, ecological, and silvicultural benefits to such a strategy.

The dearth of species and individuals in deciduous forests was surprising. The Liard Valley forests had much lower species richness (Table 7) and abundance when compared to similar forests studied in Saskatchewan by Hobson and Bayne (2000a). This disparity is because of the absence of many eastern (deciduous) species this far west and north, and a lack of western or northern species filling those niches. Species inhabiting deciduous or mixedwood stands in Saskatchewan, such as Chestnut-sided Warbler (*Dendroica pensylvanica*), Connecticut Warbler (*Oporornis agilis*), Evening Grosbeak (*Coccothraustes vespertinus*), Black-throated Green Warbler (*Dendroica virens*), Cedar Waxwing

(*Bombycilla cedrorum*) and Philadelphia Vireo were either absent or uncommon in forests in the Liard Valley.

The three other forest types studied also had interesting bird communities. Surprisingly, young, thicketlike stands of mixed deciduous and coniferous trees had the second highest relative abundance of birds in the study area (Table 5). This was because species with a bimodal abundance response to forest age (in young and old, such as American Redstart) were found here rather than in the much younger regenerating clearcuts, in addition to other species that were not typically in upland forests (e.g., Yellow-bellied Flycatcher, Fox Sparrow). The two forest types with the fewest observed species (wooded bogs and clearcuts) paradoxically had unique assemblages of species. Palm Warbler was restricted to wooded bogs, and Hermit Thrush and Dark-eyed Junco were much more common there than in other forest types, similar to communities in this forest type in Saskatchewan (Hobson and Bayne 2000a). Clearcuts had an early successional bird community not found in other forest types. Mourning Warbler, Alder Flycatcher, and White-throated Sparrow were rarely found in undisturbed forest. Wooded bogs and clearcuts may lack the diverse communities of the older, upland forests, but they are important components of the landscape to the regional bird community.

BIRD-HABITAT RELATIONSHIPS

Bird communities, not vegetation data, should be used to subdivide upland boreal forests into discrete habitats for bird-habitat analyses. To best describe bird-habitat relationships, the 80% cut-off defining monotypic forests is only adequate, often resulting in derived species lists that do not agree with field experience. (In the absence of better vegetation data, we recommend using 80% dominance by coniferous or deciduous species to divide the forest into habitats.) This variance is not surprising since canopy tree data are only part of a habitat description. Deciduous- and coniferous-associated bird communities exist across a wider range of forest types than is apparent from only the forest inventory. This is a problem for areas where there are no local bird data, increasing the statistical uncertainty in any derived relationships. Using an *a posteriori* vegetation classification that is based on field data will increase the certainty of

modeling and other habitat analyses. Admitting that stand boundaries on forest inventory maps are not always boundaries for bird territories is enough to justify *a posteriori* refinement of habitat classes.

Many bird species in the Liard Valley are plastic in their habitat use. This is common in many boreal-breeding passerines (Keast 1990, Willson and Comet 1996). Boreal species often have high abundance in two age classes of forest (Schieck and Nietfeld 1995), or respond to aspects of the habitat, such as foraging areas, that are common across various types of forest (Morse 1985). Aside from the few species mentioned in the results section, most (62%) occurred in at least three habitats, including three ubiquitous species (Magnolia Warbler, Tennessee Warbler, and Chipping Sparrow). However, this plasticity does not overshadow apparent preferences for certain forest types. Many species did show markedly higher abundances in one or two particular forest types. Examples include White-throated Sparrows in clearcuts, Yellow-bellied Flycatchers, American Redstarts, and Black-and-white Warblers in thicketlike young forests, Canada Warblers in deciduous-dominated forests, Western Tanagers (*Piranga ludoviciana*) in mixed and coniferous forests, and Dark-eyed Juncos in wooded bogs.

The results of the CCA are primarily descriptive. The vegetation variables plotted in the CCA diagram reasonably explain variation in the bird community and agree with the DCA results. Neither of the primary gradients is surprising as an important determinant of the organization of the bird community. This is also true of larger scale analyses including substantially more distinct habitats (Kirk et al. 1996; D. A. Kirk and M. Csizy, unpubl. data). The advantage of such an analysis, however, is the ability to directly read the correlation of each vegetation variable with major axes, and relate that directly to the position of a bird species or group of birds on the ordination plot. Descriptions of general habitat requirements or identification of habitat-oriented bird communities are apparent to nonspecialists. The diagram indicates that American Redstarts in the Liard Valley were found in deciduous-dominated forests that are structurally complex with open canopies and high amounts of alder. While such generalities cannot be used to make species-specific predictions, they are enough to understand which spe-

cies will be affected by significant changes in habitat.

In summary, many of the community-level patterns from other areas of the western Canadian boreal forest are present in the Liard Valley. However, the richness and relative abundance of the songbird community is lower than in similar forests farther south and east. The increasing number of standardized songbird studies in the western boreal forest is allowing specific comparisons across large regions of forest. This will permit regional-scale modeling of bird-habitat relationships in a specific enough way to help guide forest management practices. Regional studies are still needed in areas farther north, as exact range edges and relative abundances of many species are poorly described, preventing extrapolation of models from farther south. The White-throated Sparrow and Magnolia Warbler discussion exemplifies such regional differences. Furthermore, important patterns are being reinforced across the boreal region. One of the most significant is that mixedwood forests are disproportionately valuable to songbirds and must be a serious management concern.

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