AVIAN COMMUNITIES OF MATURE BALSAM FIR FORESTS IN NEWFOUNDLAND: AGE-DEPENDENCE AND IMPLICATIONS FOR TIMBER HARVESTING[1]

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Abstract. The amount of old growth balsam fir (*Abies balsamea*) forest (80+ years) in Newfoundland, Canada has declined and management towards a 60-year rotation age will further reduce the availability of old forest as wildlife habitat. We distinguished among three mature age-classes of forests (40–59, 60–79, and 80+ years) based on tree density, canopy gaps, woody debris, and moss and litter cover on the ground. Canonical correspondence analysis revealed two groups of stands: one containing all of the 40-year-old stands and most 60-year-old stands, and a second that included old growth stands and 4 of 10 60-year-old stands. Forest birds were separated into four groups: one preferring the youngest stands, another observed primarily in old stands, and two others that were intermediate. Bird species richness was greater in 40-year-old forests than in 60+ and 80+-year-old stands. Black-backed Woodpecker (*Picoides arcticus*) and Gray-cheeked Thrush (*Hylocichla minima*) were most abundant in old forests. Six other species also were grouped together with the latter two as an old forest group. We observed more species and more total birds breeding on productive forest site types than on less-productive sites based on a forest ecosystem classification, and five species showed significant relationships between density and site quality. We observed few relationships between stand age and migratory strategy. The only guild for which there was a significant relationship of abundance with forest age was cone seed-eaters, which were more common in second-growth forests than in old forest. To maintain avian diversity in these forest landscapes, some stands must be allowed to develop as old growth.

Key words: balsam fir, bird community, boreal forest, forest management, Newfoundland, old growth, species richness.

INTRODUCTION

Different avian communities occur in response to changes in vegetation structure and species composition following logging (Helle 1985, Welsh 1987, Morrison 1992). Stand-level factors that influence bird species use of a given forest include: tree species composition (Welsh 1987, Kirk et al. 1996), canopy cover (Wiens and Rotenberry 1981), foliage height profile and volume (MacArthur and MacArthur 1961), forest site type (Welsh and Lougheed 1996), stand age (Welsh 1987, Kirk et al. 1996), and specific structures such as canopy gaps and snags (Virkkala et al. 1994). However, little information is available on bird community response to an age gradient among mature boreal forest stands. Fur-

thermore, different boreal forest ecosystems support distinct avian communities (Erskine 1977, Kirk et al. 1996, Welsh and Lougheed 1996), indicating that landscape substitution of one forest type for another is not an appropriate conservation strategy to maintain bird communities. Forest managers are expected to maintain biological diversity across forested landscapes as an integral requirement of forest use. An understanding of factors that influence avian community structure is important to enable proper management. This is especially important in considering whether to reduce rotation age of the forest below the natural longevity of the dominant species.

Concern over loss of old-aged forests is common across North America (e.g., Leverett 1996). In western Newfoundland, Canada, the amount of natural-origin old balsam fir (*Abies balsamea*)

forest has been reduced primarily through logging and as a result of a lethal outbreak of hemlock looper (*Lambdina fiscellaria*) in 1987 (Thompson 1991, Newfoundland Forest Service, unpubl. data). About 26% of the area described by Rowe (1972) as the Corner Brook boreal forest region (region B28.b) is currently in the age-class > 80 years, while about 17% exists in age-class 60–80 years, as second-growth forests (i.e., re-growth following logging). Within a decade, much of the 80+ year age-class will either be harvested or die and revert to young forest because balsam fir is a short-lived species. With ongoing harvesting, there will be little old forest within 10 to 20 years. Harvesting some of the next 60+ year age-class (now 40–60 years old) for pulpwood is inevitable, particularly because many of these forests were pre-commercially thinned, enabling more rapid growth than in naturally self-thinning forests. Already some of the younger stands are being harvested because of their accessibility and high rates of re-growth on good sites (W. Brown, Corner Brook Pulp and Paper, pers. comm.). Moving to a younger rotation age for balsam fir forests will undoubtedly have consequences for biological diversity, but as noted by Haney and Schaadt (1996), truncation of forest age is rarely discussed with respect to wildlife response. Thompson and Curran (1995) showed that there were differences in the mammalian communities between 80+-year-old uncut and 60–79-year-old second growth stands, and that two species, (marten *Martes americana* and meadow voles *Microtus pennsylvanica*), occurred only in older, natural-origin forests.

This study reports on songbird communities breeding in balsam fir ecosystems of western Newfoundland. Newfoundland's balsam fir forests are different from most boreal forest types because they do not require fire to regenerate naturally, and the ecosystems do not undergo dramatically different successional stages following logging (Bakuzis and Hansen 1965). Instead, they progress through a series of age-classes dominated by balsam fir at decreasing densities, ranging from > 20,000 stems ha⁻¹ as shrubs, to older stands with tree densities of about 2,000 ha⁻¹ (Meades and Moores 1989, Thompson and Curran 1995). Balsam fir stands are short-lived and the old-growth stage may last only 20–30 years, with trees older than 100 years being exceptional. Little empirical information is available for forest bird communities

in Newfoundland balsam fir ecosystems, although Whitaker and Montevecchi (1997) compared birds in riparian areas and interior forests, from the same general area as our study. Our research objective was to determine whether there were distinct avifaunas among mature stands of various ages in balsam fir forests. We also examined the possibility that some members of the avian community were old-growth dependent. These populations could be affected by a decline in the oldest age-class, as the forest industry continues to move to a rotation age of about 60 years. Our null hypothesis was because these forests appear so similarly structured at all ages older than pole-sized, there would be no difference in the avian communities among stands aged 40+ years (young mature), 60+ years (mature), or 80+ years (late mature). We suspected that differences would be least likely between stands aged 60–79 and 80+ years, where there appeared to be little difference in stand density or height (Thompson and Curran 1995).

Balsam fir forests occupy a range of sites that vary in their productivity (Meades and Moores 1989). Site types are distinguishable based on ground cover, ranging from moss-dominated poor sites to rich sites dominated by a layer of herbaceous plants and ferns. Welsh and Lougheed (1996) determined that breeding bird communities differed along gradients of stand productivity, and that habitat specialization of species was common in Ontario black spruce (*Picea mariana*) and mixedwood forests. Their study area had a higher tree species richness and greater range of site types than did our balsam fir sites in western Newfoundland. We tested the relationship between avian species richness and certain forest types defined by Meades and Moores (1989).

METHODS

STUDY AREA AND STAND SELECTION

We chose 35 stands over a large area of the Newfoundland west coast balsam fir forest type (Rowe 1972), extending about 140 km north to south, from the upper Humber River valley (49°37′N, 57°12′W), to the immediate south and west of Little Grand Lake (48°35′N, 57°50′W). Stands were chosen based on age-classes and tree species associations determined from forest resource inventory mapping and industrial cut-

ting records. Stands ranging in age from 40 to 47 years since logging were pooled into age-class 40 ($n = 12$); those stands 52 to 73 years since logging were called age-class 60 ($n = 10$); and uncut stands that had not been logged and ranged from 77 to 87 years, were our age-class 80 ($n = 13$). We based forest ages on the mean of 20 randomly sampled trees per stand, after determining approximate ages from forest resource mapping. Our stands were randomly selected from those available, but choice was constrained by several criteria and stand accessibility. To eliminate possible area effects, selected stands were not fragments isolated by edges of recently logged stands, and were part of larger forest complexes of a minimum size of 3 km², although one edge of many stands was often adjacent to a road. The 13 uncut stands were located in the upper Humber River valley and near Little Grand Lake. In these two areas, stands were distinctly separated by lakes and bogs, but were located within a radius of a few kilometers of each other. Individual stands were a minimum of 25 ha and were defined by forest site types and borders with other distinct forest habitats, such as bog forests, or riparian zones. In each stand we established five bird census points 200 m apart and a minimum of 100 m from edges. Mean forest site index was determined by classifying each census point at five locations: one at the census point and four others 25 m away in each of the four cardinal directions, using tabular site values from Meades and Moores (1989). Site index referred to production of wood volume per unit area, and reflected soil moisture and fertility conditions. We attempted to choose stands that had one consistent site type throughout the entire stand, but when this was impossible, we calculated a mean site type for the stand that was proportional to the amount of each site type at the bird census points. Site index was used to pool sites as either "rich" with a site index of > 9.0, or "poor" where site index was < 8.9 (Meades and Moores 1989).

MEASUREMENT OF HABITAT VARIABLES

We characterized forest stands by density and species composition of vegetation, canopy cover, standing dead trees, ground cover, and woody debris on the forest floor. Stem density of trees (diameter at breast height, dbh, > 10 cm), small trees (> 3 m tall and < 10 cm dbh), shrubs (1–3 m tall), and dead trees (stem height > 3 m)

was measured using the plotless point-distance technique of Batcheler (1975), at 100 points per stand. The points were located about 20 m apart on five random transects in each stand. We recorded height, dbh, and species for each stem. These data provided the variables: total stem density, species stem densities, mean tree height, coefficient of variation in tree height (a measure of canopy profile), and proportion of trees in various stem size-classes (e.g., snags > 20 cm). We examined ground cover on 50 2-×-2 m quadrats chosen arbitrarily about 30 m apart, along five random transects per stand. For each quadrat, we subjectively estimated percent cover for four horizontal layers: (1) graminoids (grasses, sedges, and rushes), lichens, feather mosses, *Sphagnum* mosses, rock, exposed soil, litter (dead non-woody material), and twigs and branches (slash), (2) flowering plants and ferns, (3) low shrubs and small ferns (10–50 cm), and (4) medium shrubs and tall ferns (predominantly *Dryopteris spinulosa*) (0.5–1 m). Woody debris was defined as logs > 10 cm diameter, and were counted on 10 equilateral triangular 90-m transects (30 m on a side) per stand (McRae et al. 1979) on a subsample of five stands in each age-class. Percent canopy closure was measured with a forest densiometer at the same 50 locations per stand locations chosen for ground quadrats.

BIRD CENSUS

We censused birds by song, or if seen, at five permanent points per stand, twice each year, before 10:30, between 9 June and 9 July, in 1991 and 1992, following procedures of D. A. Welsh (pers. comm.), which were a modification of the unlimited distance point-count method of Blondel et al. (1981). Two experienced bird observers censused different stands simultaneously, and the same observer visited the same points in both years. Each observer waited 2 min after arriving at each point, and then recorded all species seen or heard during a 10-min sampling period. We did not survey during rain or if wind exceeded 20 km hr⁻¹. The census method assumed equal species detectability among points, stands, and observers. Our index of abundance for each species per point was calculated by using the largest value from the two censuses, and these values were summed for each of the five points to provide stand totals, in each year (Welsh and Lougheed 1996).

DATA ANALYSIS

We compared individual habitat variables among forest age-classes by 2-way ANOVA, in order to characterize differences among the stands. We then used least significant difference tests (LSD; Day and Quinn 1989) to test for differences between forest ages.

We eliminated bird species from our analyses if they occurred only in one stand, were likely not breeding, or were only recorded as flying over a stand. We examined for differences in individual log-transformed species abundances between years by ANOVA, and combined data from the two years as a mean abundance of each species per stand for subsequent analyses. To examine for possible differences in bird species among forest age-classes, forest site types, or an interaction term, we constructed a 2-way factorial ANOVA model. To improve sample size, we pooled four forest site types into two site types for this analysis: poorer sites (fern/moss and moss) and richer sites (fern/herb and fern) (site types from Meades and Moores 1989).

We used Pearson correlation analysis followed by principal components analysis to reduce the forest vegetation data set to a reasonable number of variables (i.e., variables that may be most important to birds, and to ensure that the number of variables was less than the number of plots [ter Braak 1986]). To ordinate the matrices of bird communities and forest stand description variables, selected variables were then entered into a canonical correspondence analysis (CCA), instead of the often-used detrended correspondence analysis, based on the recommendations of Palmer (1993). Although Palmer suggested that CCA performs well even if variables are correlated and non-normal, we used uncorrelated and normalized variables following the recommendations of ter Braak (1986, 1994). We interpreted the distribution of bird communities along CCA axes by examining loadings of key vegetation variables on the eigenvectors, and by plotting bird species and forest stands against the first two CCA axes. Bird communities were grouped using TWINSPAN (Hill 1979) to improve interpretation of the ordination graph.

We used 2-way ANOVA to test for possible differences in occurrence among various guilds of species which were based on foraging strategies and nesting strategies: flycatching, foliage or trunk gleaning, ground feeding, pecking, cone seed eating, shrub nesting, and ground nesting. For these tests, we looked at differences in guild abundance in two age categories: old forest vs. second growth forest (i.e., 40-year and 60-year stands pooled). Finally, we examined whether individual forest stands were selected on the basis of age in relation to individual species' migratory strategies: resident, short-distance migrant, or long-distance (Neotropical) migrant, as has been suggested for boreal passerine birds in western and northern Canada (Kirk et al. 1996). Migratory strategies for Newfoundland species were taken from MacTavish et al. (1989). Results are presented as mean ± SE, with a significance level of $P < 0.05$.

RESULTS

Despite a similarity in appearance, several variables differed among the age-classes of forest stands (Table 1). Compared to either 40- or 60-year age-class stands, uncut old forest stands had a more open structure with lower tree and small tree stem density, more gaps, fewer deciduous small trees (white birch *Betula papyrifera* and pin cherry *Prunus pensylvanica*), a more varied tree height profile, shorter small trees, larger diameter living and dead trees, and more dead wood on the ground. Canopy cover was significantly lower in old stands compared to 60-year-old stands, but similar in the 40- and 60-year age-classes. Ground cover in 80-year-old stands had less litter and more mosses than all younger stands, and more small shrubs (mostly young balsam fir in forest gaps) than were found in 40-year-old stands. More litter and less moss also distinguished 40-year-old stands from 60-year-old stands, along with less woody debris, higher tree and small-tree density, higher density of small deciduous trees, smaller diameter of dead trees, and a more variable small tree height. Interestingly, mean tree height did not change from 40 to 80 years of age: 11.2 ± 0.4 m, 11.3 ± 0.5 m, and 11.9 ± 0.4 m, in 40-, 60-, and 80-year age-classes, respectively. Similarity in height and the dominance by balsam fir was why the stands appeared similar, regardless of age. Small gaps created by fallen trees, either individually or in small groups, were common only in the oldest forests as indicated by lower canopy cover, lower tree density, high percent of low-shrub ground cover, and more woody debris.

TABLE 1. Mean ± SE of important attributes of balsam fir forest stands of three age-classes from western Newfoundland, where forest songbirds were censused in 1991–1992, with significant univariate differences by ANOVA followed by LSD comparisons between pairs. Means followed by the same letter were not significantly different among age-classes. (n = 12, 10, and 13 stands, for 40-, 60-, and 80-year age-classes, respectively.)

Variable	Second growth		Uncut 80+ years	F	P
	40+ years	60+ years			
Ground cover (%):					
Shrubs < 1 m tall	6.5 ± 1.1A	8.5 ± 1.6AB	10.0 ± 0.9B	2.59	0.09
Slash[a]	6.9 ± 0.8A	8.6 ± 0.7AB	9.1 ± 0.6B	2.77	0.08
Litter	45.6 ± 4.5A	32.7 ± 2.6B	22.5 ± 1.9C	7.17	0.003
Mosses[b]	36.8 ± 1.7A	52.7 ± 6.2B	59.7 ± 2.1C	4.99	0.01
Stand variables:					
Canopy cover (%)	72.7 ± 1.6AB	74.3 ± 2.2B	68.9 ± 1.7A	2.32	0.10
Woody debris (logs 90 m^{-1})	3.3 ± 0.1A	6.4 ± 0.3B	14.0 ± 1.4C	6.73	0.003
Tree density (stems m^{-2})	0.21 ± 0.08A	0.15 ± 0.01B	0.12 ± 0.01B	6.65	0.004
Small tree density (stems m^{-2})	0.33 ± 0.07A	0.12 ± 0.02B	0.07 ± 0.02C	12.50	<0.001
Deciduous small tree density (stems m^{-2})	0.06 ± 0.01A	0.02 ± 0.01B	0.01 ± 0.01C	57.27	<0.001
Shrub density (stems m^{-2})	0.26 ± 0.07A	0.18 ± 0.06B	0.23 ± 0.05A	2.41	0.09
Dead tree and small tree density (stems m^{-2})	0.16 ± 0.02A	0.14 ± 0.02A	0.08 ± 0.01B	5.24	0.01
Mean tree diameter (cm)	14.4 ± 0.8A	15.7 ± 0.9A	17.2 ± 1.3B	4.81	0.02
Mean dead tree diameter (cm)	5.9 ± 0.5A	7.6 ± 0.5B	11.9 ± 0.5C	39.94	<0.001
Coefficient of variance of tree height	0.16 ± 0.01A	0.18 ± 0.02A	0.26 ± 0.01B	14.53	<0.001
Small tree height (m)	6.3 ± 0.2A	6.9 ± 0.4A	5.5 ± 0.2B	8.74	0.005
Coefficient of variance of small tree height	0.33 ± 0.01A	0.28 ± 0.02B	0.33 ± 0.01A	6.34	0.01

[a] Dead twigs and branches < 10 cm diameter.
[b] Predominantly *Pleurozium schreberi, Hylocomium splendens,* and *Spahagnum* spp.

We recorded 42 bird species, with 10 comprising about 80% of the birds counted in both years (Table 2, asterisked [*] species). The mean abundance of most species was constant between years, although six species were significantly more abundant in one year or the other: Northern Flicker, Olive-sided Flycatcher, and Common Redpoll for which there were no observations in 1992 (see Table 2 for common and Latin nomenclature); Yellow-bellied Flycatcher (1.97 ± 0.27 birds point^{-1} vs. 2.65 ± 0.39, in 1991 and 1992, respectively), Tree Swallow (0.04 ± 0.03 vs. 0.01 ± 0.01), and Golden-crowned Kinglet (1.08 ± 0.2 vs. 0.51 ± 0.15). Two of these six species were not used in the analyses (Tree Swallow and Common Redpoll), and we combined results from the two years because so few differences were found in the total community. There were sufficient observations to conduct analyses for 32 species.

Most of the differences that we observed in bird species among forest age-classes were between the 40- and/or 60-year-old stands and old uncut forests (Table 2). Five species were most

common in the younger age-classes compared to the uncut old forests, including: Boreal Chickadee, Black-throated Green Warbler, Fox Sparrow, Purple Finch, and Pine Siskin. Species more abundant in the 40-year age-class than in the 60-year age-class included: Black-capped Chickadee, Ovenbird, Magnolia Warbler, Northern Waterthrush, and Pine Grosbeak. We found similar densities of Yellow-rumped Warbler, White-throated Sparrow, and Dark-eyed Junco in 40- and 60-year age-classes, but these three species were more abundant in 80-year-old than 40-year-old stands. Ruby-crowned Kinglets increased in abundance with stand age and were most common in old forest. No species was most abundant in the 60-year age-class. We recorded two species that were associated only with old uncut forests: Black-backed Woodpecker (except one bird seen in a 60-year-old stand) and Gray-cheeked Thrush. Both of these species were rare.

Species richness was significantly higher in the 40-year age-class compared to either 60- or 80-year age-classes (9.17 ± 1.00 vs. 7.39 ± 1.22

TABLE 2. Mean abundance ± SE of species recorded per point by forest age-class in Newfoundland balsam fir forests, 1991–1992, and significant differences by ANOVA among the age-classes and LSD between-pair comparisons, site types (rich, poor), and the interaction term between age and site type. Values followed by a different letter were significantly different among age-classes.

Species[a]	Migratory Status[b]	Guild[c]	Second growth 40+ years	Second growth 60+ years	Uncut 80+ years	F	P	P Age	P Site	P Age*site
Downy Woodpecker Picoides pubescens	R	P	0.20 ± 0.08	0.04 ± 0.04	0.11 ± 0.06					
Black-backed Woodpecker Picoides arcticus	R	P	0A	0.01A	0.17 ± 0.09B	4.95	0.01	0.001		
Northern Flicker Colaptes auratus	SD	P	0.08 ± 0.04	0	0.02 ± 0.02					
Olive-sided Flycatcher Contopus borealis	LD	F	0.04 ± 0.04	0	0.14 ± 0.08					
Yellow-bellied Flycatcher* Empidonax flaviventris	LD	F	2.08 ± 0.20	1.76 ± 0.26	2.08 ± 0.27					
Gray Jay Perisoreus canadensis	R	—	0.35 ± 0.11	0.23 ± 0.09	0.31 ± 0.11					
Black-capped Chickadee Parus atricapillus	R	FG	0.53 ± 0.11A	0.14 ± 0.08B	0.24 ± 0.07AB	3.15	0.05	0.02		
Boreal Chickadee Parus hudsonicus	R	FG	0.68 ± 0.17A	0.71 ± 0.27A	0.11 ± 0.06B	8.36	0.01	0.002		
Brown Creeper Certhia americana	R	FG	0	0.04 ± 0.04	0.06 ± 0.04					
Winter Wren Troglodytes troglodytes	SD	GG	0.03 ± 0.03	0.04 ± 0.04	0.21 ± 0.12					
Golden-crowned Kinglet* Regulus satrapa	R	FG	1.05 ± 0.19	1.00 ± 0.16	1.05 ± 0.19					
Ruby-crowned Kinglet* Regulus calendula	SD	FG	1.38 ± 0.16A	1.52 ± 0.25B	2.37 ± 0.37C	3.39	0.04	0.01		
Swainson's Thrush* Catharus ustulatus	LD	GG, SN	2.06 ± 0.40	1.28 ± 0.32	2.06 ± 0.22					
Hermit Thrush Catharus guttatus	SD	GG, GN	0.13 ± 0.07AB	0A	0.37 ± 0.20B	2.65	0.09	0.05		
Gray-cheeked Thrush Hylocichla minima	LD	GG, SN	0A	0A	0.13 ± 0.06B	4.46	0.02	0.01		
American Robin* Turdus migratorius	SD	GG	1.23 ± 0.33	0.88 ± 0.28	0.56 ± 0.17					

TABLE 2. Continued.

Species[a]	Migratory Status[b]	Guild[c]	Second growth		Uncut 80+ years	F	P	P		
			40+ years	60+ years				Age	Site	Age*site
Magnolia Warbler *Dendroica magnolia*	LD	FG, SN	0.45 ± 0.10A	0.28 ± 0.21B	0.42 ± 0.17AB	3.30	0.05	0.05		0.03
Yellow-rumped Warbler* *Dendroica coronata*	SD	FG	2.28 ± 0.27A	2.83 ± 0.23AB	3.41 ± 0.37B	2.80	0.07	0.05		
Black-throated Green Warbler* *Dendroica virens*	LD	FG	3.86 ± 0.53A	2.46 ± 0.56AB	1.34 ± 0.23B	11.08	<0.001	0.05	0.01	0.001
Bay-breasted Warbler *Dendroica castanea*	LD	FG	0.21 ± 0.08	0	0.03 ± 0.03					
Blackpoll Warbler *Dendroica striata*	LD	FG	0.23 ± 0.11	0	0.11 ± 0.07					
Black and White Warbler *Mniotilta varia*	LD	FG, GN	0.04 ± 0.04	0	0.21 ± 0.13					
Ovenbird* *Seiurus aurocapillus*	LD	GG, GN	2.27 ± 0.35A	1.14 ± 0.41B	0.25 ± 0.10C	18.81	<0.001	0.001	0.03	0.03
Northern Waterthrush* *Seiurus noveboracensis*	LD	GG	0.89 ± 0.23A	0.29 ± 0.16B	1.00 ± 0.25A	3.52	0.04	0.05		
Mourning Warbler *Oporornis philadelphia*	LD	FG, GN	0.27 ± 0.18	0.19 ± 0.11	0.28 ± 0.11	4.64	0.02		0.01	
Fox Sparrow *Passerella iliaca*	SD	GG, GN	0.57 ± 0.17A	0.48 ± 0.20A	0.16 ± 0.12B	3.71	0.04	0.05		
White-throated Sparrow* *Zonotrichia albicollis*	SD	GG, GN	0.92 ± 0.19A	1.27 ± 0.35AB	1.94 ± 0.36B	8.68	0.001	0.05	0.001	0.02
Dark-eyed Junco *Junco hyemalis*	R	GG	0.02 ± 0.02A	0.12 ± 0.12AB	0.18 ± 0.08B	2.11	0.14	0.06		
Pine Grosbeak *Pinicola enucleator*	R	CS	0.55 ± 0.13A	0.19 ± 0.09B	0.15 ± 0.07B	4.48	0.02	0.04		0.05
Evening Grosbeak *Coccothraustes vespertinus*	SD	CS	0.02 ± 0.02	0	0.04 ± 0.04					
Purple Finch *Carpodacus purpureus*	R	CS	0.64 ± 0.19A	0.36 ± 0.12A	0.02 ± 0.02B	7.74	0.002	0.002		
Pine Siskin *Carduelis pinus*	R	CS	0.69 ± 0.14A	0.91 ± 0.26A	0.31 ± 0.10B	3.61	0.04	0.01		

[a] Species recorded but omitted from analyses: Common Raven *Corvus corax*, American Crow *Corvus brachyrhynchos*, White-winged Crossbill *Loxia leucoptera* (fly-overs), Tree Swallow *Tachycineta bicolor*, Red-breasted Nuthatch *Sitta canadensis*, Tennessee Warbler *Vermivora peregrina*, Lincoln's Sparrow *Melospiza lincolnii*, Solitary Vireo *Vireo solitarius*, Common Redpoll *Acanthus flammea* (< 3 sites). Asterisk (*) indicates 10 most common species.
[b] R = resident, SD = short distance migrant, LD = long distance migrant, from MacTavish et al. (1989).
[c] P = pecking, F = flycatching, FG = foliage or trunk gleaning, GG = ground feeders, CS = cone seed foraging, GN = ground-nesting, SN = shrub-nesting.

vs. 7.39 ± 0.77 species point^{-1}, in 40-, 60-, and 80-year classes, $F_{2,32} = 5.54$, $P < 0.01$). There also was a significantly higher avian species richness on rich sites (8.74 ± 0.66) than on poor sites (7.12 ± 0.72) ($F_{1,33} = 10.28$, $P = 0.003$). Total bird abundance was 4.78 ± 0.19, 3.64 ± 0.23, and 4.04 ± 0.18 birds point^{-1}, in 40-, 60-, and 80-year classes, respectively, $F_{2,32} = 2.60$, $P = 0.09$), with significantly more birds in the 40-year age-class than in the 60-year age-class (LSD test, $P = 0.03$). There were significantly more birds on rich sites (23.7 ± 0.7) than on poor sites (17.7 ± 0.6) ($t_{33} = 3.21$, $P = 0.003$).

Four bird species were significantly more abundant on rich sites than on poor sites: Black-throated Green Warbler, Ovenbird, Mourning Warbler, and White-throated Sparrow (Table 2). For five species, there was a significant inter-action effect between forest age and site type. A visual examination of scatter plots of abundance of these species plotted individually against forest age and site type, showed that for Magnolia Warbler, Black-throated Green Warbler, White-throated Sparrow, and Pine Grosbeak, observations were divided between rich and poor sites in 40- and 60-year age-classes, but most observations in the 80-year age-class were from rich sites. For Ovenbirds, observations were split equally between poor and rich sites in 40- and 80-year classes, but in the 60-year age-class most birds were observed on richer sites.

The CCA separated the 35 forest stands into two clear groups (Fig. 1) along the first two axes. One group comprised all of the 40-year stands and most of the 60-year stands, whereas a second group included all of the old uncut stands and four of the 60-year-old second-growth stands. The first CCA axis represented a gradient based on variables related to forest age including significant correlations ($P < 0.05$) with declining density of deciduous stems, increased logs on the ground, increased diameter of standing dead trees, increased tree height, greater percent ground area covered by tall ferns, and decreased small-tree density. The second axis represented a site richness gradient, with the richer sites with more ferns, low ($<$ 1 m) shrubs, and forbs towards the bottom of the plot, and poorer sites towards the upper end.

TWINSPAN distinguished four groups of birds, and these were visible when bird species were plotted on the first two CCA axes (Fig. 1). The first group of six species was most common in youngest stands (Table 2). Two groups occurred near the graph centroid and contained more than half the species that we recorded. These groups included species that were generally common to all stands, although group 2 contained some species most common in the two younger age-classes, such as Fox Sparrows. Group 3 contained some species that were most common in either 40- or 80-year-old forests, including Hermit Thrush and Northern Water-thrush. A fourth group was spread widely along the richness axis, but concentrated on the old-stand end of axis 1, and it included the two species found only in old forests, Black-backed Woodpeckers and Gray-cheeked Thrushes.

We observed few differences in stand selection by species according to their migratory status as resident, short-distance migrant, or long-distance (Neotropical) migrant. Five of 11 resident species were found significantly more often in young forests compared to older forests, whereas three were most common in old forests, and three showed no preferences. Of nine short-distance migrants, six showed preferences, and of these, three were in older forests. Five of 12 long-distance migrants were found in significantly greater numbers among the age-classes and these were equally divided between 40- and 80-year-old stands (Table 2).

The cone seed-eating guild showed a significant preference for second-growth forests compared to old forests (mean abundance = 0.75 ± 0.21 in old forests vs. 1.82 ± 0.33 in second growth forest, $F_{1,33} = 7.67$, $P < 0.01$). We found no significant difference in abundance for any other guild among the stand ages, and none of our guilds was represented by the CCA ordination or among the TWINSPAN groups.

DISCUSSION

Compared to other boreal forest types, the lack of difference in tree species composition between young-mature and over-mature age-classes is unusual (Rowe 1972), as is the short-lived nature of old-growth balsam fir forests (Bakuzis and Hanson 1965). The major differences among the age-classes of forests that we studied were related to ground cover (including logs), stem densities, density of deciduous small trees, and stand openness. The 40-year age-class stands were characterized by a well-developed small-tree layer that had a relatively high deciduous component (although it was only 6% of
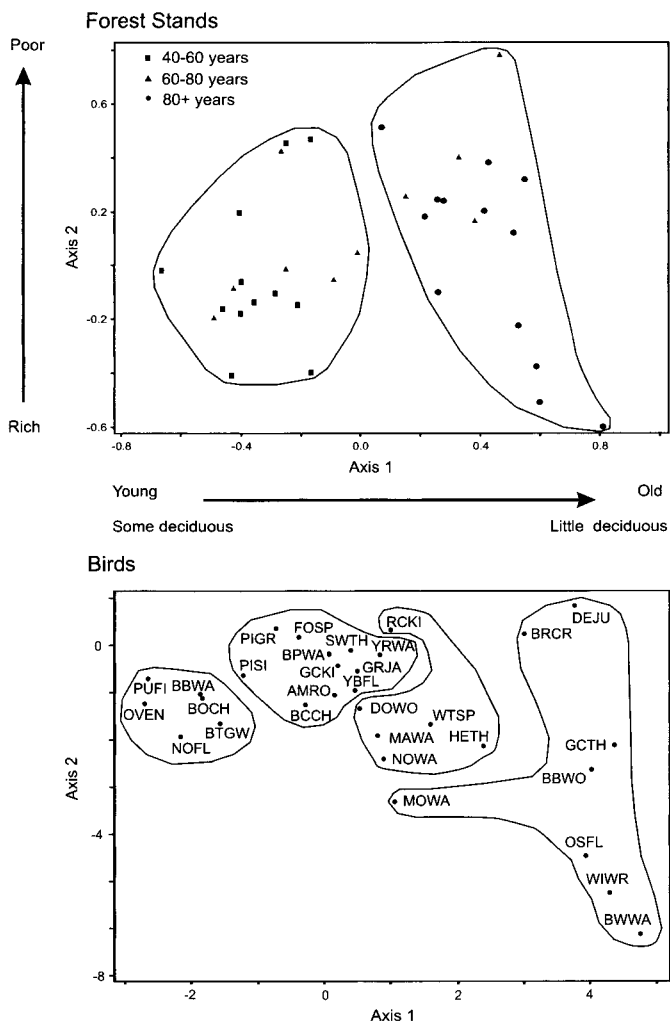
FIGURE 1.   Plot of balsam fir stands and their associated breeding bird communities along the first two axes of a canonical correspondence ordination. Groups portrayed were determined by TWINSPAN. Bird species are coded as follows (alphabetically): AMRO, American Robin; BBWA, Bay-Breasted Warbler; BBWO, Black-backed Woodpecker; BCCH, Black-capped Chickadee; BOCH, Boreal Chickadee; BPWA, Blackpoll Warbler; BRCR, Brown Creeper; BTGW, Black-throated Green Warbler; BWWA, Black and White Warbler; DEJU, Dark-eyed Junco; DOWO, Downy Woodpecker; FOSP, Fox Sparrow; GRJA, Gray Jay; GCTH Gray-cheeked Thrush; HETH, Hermit Thrush; MAWA, Magnolia Warbler; MOWA, Mourning Warbler; NOFL, Northern Flicker; NOWA, Northern Waterthrush; OSFL, Olive-sided Flycatcher; OVEN, Ovenbird; PIGR, Pine Grosbeak; PISI, Pine Siskin; PUFI, Purple Finch; RCKI, Ruby-crowned Kinglet; WTSP, White-throated Sparrow; YBFL, Yellow-bellied Flycatcher; YRWA, Yellow-rumped Warbler.

small-tree stems) that was mostly absent from older stands (< 1% of stems). The two most abundant deciduous tree species, white birch and pin cherry, are extremely short-lived and most are gone by the time the forest is 80 years old. Tree and small-tree density exhibited a gradient from highest in youngest stands to lowest in oldest stands. Forest stands in the 60-year age-class

were the most simple in terms of their structure, with a lower deciduous component than the 40-year group, and fewer large dead stems and a less open canopy than the old forests. Older stands were characterized, relative to the two younger age-classes, as being somewhat more open, larger standing dead trees, and the most large woody debris on the ground. Many of

these characteristics are common to other old-growth forest ecosystems (Leverett 1996), but clearly less accentuated in the forests of western Newfoundland because of the enormous dominance by short-lived, relatively small balsam fir. An important difference in terms of nesting substrate for some bird species, and as cover for ground-feeders, was the presence of a significantly higher density of shrubs in the 40-year and 80-year stands than in 60-year-old stands, and the well-developed low shrub layer (i.e., < 1 m) in older forests compared to in either of the second-growth age-classes. Canopy cover was about 10 to 20% higher in these forests compared to other boreal forest types (Welsh 1987), even in the oldest age-class. Despite these relatively subtle differences among the age-classes of mature balsam fir stands, there were significant differences in the forest bird communities supported by each.

In eastern Canadian mainland boreal forests at a latitude similar to our study area, more than 70 breeding songbird species are commonly recorded (Erskine 1977, Welsh 1987, Welsh and Lougheed 1996). In Newfoundland, we recorded just 42 species, of which less than half were abundant. This richness is similar to that from higher latitude boreal forests (Carbyn 1971, Tull et al. 1974, Willson and Comet 1996). The cold maritime climate, island location, and relatively simply-structured forest ecosystems were probable factors that combined to affect species richness. We recorded the greatest bird species richness in young-mature forest stands, and lower richness in oldest forests. Three key habitat elements were likely responsible for this result: a relatively high density of small deciduous trees, more litter, and a high shrub density in 40-year age-class stands compared to either older age-class. Other authors also have attributed increased species richness to a deciduous tree component and deciduous litter (Erskine 1977, Willson and Comet 1996), but in many studies, such a relationship may have been masked by site productivity factors (Erskine 1977, Nilsson 1979, Helle 1985), or perhaps by versatility in habitat selection among many northern bird species (Haila and Jarvinen 1990, Keast 1990).

For 17 of 32 species, we observed no clear habitat selection based on either forest age or site type. However, forest age was an important predictor of forest bird community structure among mature forest stands for the other 15

songbird species. Forest age often is correlated with stand structures that certain bird species require as nesting or foraging substrates (Helle 1985, Haney and Schaadt 1996).

We observed five common trends with age of forest. The first was a gradient of declining abundance in birds with forest age, that was probably related to the decline in deciduous small tree component and deciduous litter, as suggested by the CCA ordination (Ovenbird, Black-throated Green Warbler, Purple Finch). Titterington et al. (1979) found that Ovenbirds preferred younger spruce-fir forests in Maine, although elsewhere in the USA this species is considered an indicator of interior-mature deciduous forests (Villard et al. 1994). The second was a gradient of increase in abundance of certain species with age of stand (Ruby-crowned Kinglet, Yellow-rumped Warbler, Dark-eyed Junco), that for some may be related to abundance of large diameter trees or dead trees, probably as foraging substrates. Third, some species were similarly abundant in 40- and 80-year-old forests but were scarcer or absent in 60-year-old forests (White throated Sparrow, Black-capped Chickadee), which was likely related to stand openness and shrub abundance. Shrub cover declined from 40 to 60 years but increased again after 80 years, and was undoubtedly important to White-throated Sparrows (Erskine 1977). Fourth, some species were least abundant in old forests but similarly abundant in either 40- or 60-year-old stands, including Boreal Chickadees. We speculated that the latter species may have preferred the younger stands because of the high density of spiders, reportedly their favored food (Ficken et al. 1996), that appeared to be most abundant in forests with a dense understory of small trees (I. Thompson, pers. observ.). The final trend was for two species, Gray-cheeked Thrush and Black-backed Woodpecker, to only or predominantly occur in old forests. For Black-backed Woodpeckers, use of old forests is most likely related to large-diameter living, dead, and fallen trees (Yunich 1985, Villard 1994). This species was observed foraging on fallen logs in the old forests during a companion study (Setterington 1997). Gray-cheeked Thrushes prefer older, black spruce dominated forests elsewhere in Newfoundland (B. MacTavish, pers. comm.) and in mainland forests (Godfrey 1986). Some other species, such as Olive-sided Flycatcher, Dark-eyed Junco, Winter Wren, Hermit Thrush, and

Black and White Warbler also may have preferred old forests, but our sample sizes were too small to detect this.

In summary, species that preferred a deciduous component, deciduous litter and/or a high density of shrubs were most abundant in the 40-year age-class; those that preferred a lower density forest with a high density of larger trees and snags or shrub cover were most common in the older forests; and 16 species (50% of those in the analysis) with a wide tolerance for habitats, which we called generalists, were found to be similarly common in all age-classes. Our results with respect to generalists were similar to the high proportion of boreal forest generalist bird species reported from other studies (Keast 1980, Welsh and Lougheed 1996).

Erskine (1977) reported 10 bird species that were characteristic of balsam fir stands in mainland boreal areas. Three of the 10 were absent in Newfoundland and 5 were found commonly in balsam fir but not necessarily in all mature age-classes, such as Purple Finch, Ovenbird, and Black-throated Green Warbler. Another of Erskine's fir indicator species, Red-breasted Nuthatch, was uncommon in our stands, although Whitaker and Montevecchi (1997) found them regularly on their nearby study area 3 years later. Some species exhibited unusual habitat selection in Newfoundland compared to that reported elsewhere. For example, Dark-eyed Juncos and Yellow-rumped Warblers are often reported as habitat generalists, but we found these species to be significantly less abundant in younger mature forests than in older stands.

Site productivity influenced total bird abundance, species richness, and habitat selection by some species in Newfoundland balsam fir forests. No soils of western Newfoundland are especially productive (Damman 1964), so it is not surprising that only four species differed by site richness. Welsh and Lougheed (1996) reported that forest site richness influenced bird community structure and richness in boreal black spruce (*Picea mariana*) forests of Ontario. In that study, soils were less poor and, unlike our area, a strong deciduous component occurred on many of their richer site types influencing avian species occurrence.

Most resident bird species inhabited young mature stands, although not exclusively, whereas Neotropical migrants showed little preference among mature forest stand ages. Willson and

Comet (1996), Welsh and Lougheed (1996), and de Graaf et al. (1998) found that a higher proportion of long-distance migrants used deciduous than coniferous forests. Kirk et al. (1996) reported that the highest number of Neotropical migrants used old forests, young stands were used predominantly by short-distance migrants, and there was a tendency for resident species to occur in older forests although these species were found in all stand ages. Our results contrasted with these findings, but this may be because we did not examine the full range of stand ages, nor did we compare balsam fir forests to forests with a higher deciduous component, such as those in central Newfoundland, for which only limited information exists on bird communities.

Most studies have examined bird communities and forest succession across a much broader spectrum of forest ages than we did (Titterington et al. 1979, Welsh 1987, Helle and Mönkkönen 1990). Habitats in those studies were markedly different in structure between age groups or treatments, particularly because shrub and sapling categories were included. Therefore, it is not surprising that the unanimous conclusion from these past studies was that successional stage influences bird community composition. We examined only the old end of a true successional gradient (the last 40+ years) and yet reached the same conclusion. There are important differences in mature forest habitats as they age that are related to which species of birds will use them, and at what density. Virkkala (1991) noted that intensive forest management in Finland has resulted in declines of several bird species, especially hole-nesters that required older forests. A distinct bird community in old-growth balsam fir forests supports the argument advanced by Thompson and Curran (1995) for mammals that, in Newfoundland, old balsam fir forests constitute unique wildlife habitats. Old-growth balsam fir forest is not the kind of diverse, floristically rich forest that one may generally associate with the term "old growth." Nonetheless, planning of forest management must recognize the distinct animal communities associated with these stands, if maintaining forest biodiversity is an objective. Furthermore, because many species were most abundant on the most productive forests sites, a stratification of stands that would be allowed to become old growth is needed to ensure that certain of these

habitats are optimal. Finally, a common management practice in Newfoundland forests is to pre-commercially thin stands at about 15–20 years of age to promote growth of the conifer trees by reducing competition for light and nutrients. This practice results in the selective removal of deciduous tree species. Our results clearly showed the importance to bird species richness of the small deciduous component in balsam fir forests. Therefore, in pre-commercially thinned stands, maintaining most or all of the deciduous component is an important consideration for conserving bird diversity in western Newfoundland forests.

We observed a distinct old-growth bird community that could serve as indicator species for this forest type. Our stands were located within forest complexes, typical of boreal landscapes that are actively managed. The presence of Black-backed Woodpeckers, Gray-cheeked Thrushes, and possibly some others such as Dark-eyed Juncos and Hermit Thrushes, would indicate a range of conditions that occur within such forests including, for example, large snags, large conifer trees, forest gaps, and shrub growth within gaps. Among these species, Black-backed Woodpeckers commonly occurred at low numbers. This may have been a result of stand features, such as snags, and landscape features such as sufficient habitat availability within a given area (Angelstam and Mikusinski 1994). Further work is required to determine factors that influence populations of rare species, such as Black-backed Woodpeckers, at the landscape scale, to provide an answer to questions about stand sizes and total habitat availability within a given landscape for planning purposes.

ACKNOWLEDGMENTS

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