The effects of stand age on avian communities in aspen-dominated forests of central Saskatchewan, Canada

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Abstract

Timber harvest projections for aspen-dominated forests in the prairie region of Canada include a truncation of the current age distribution, whereby old stands of fire origin will become rarer on the landscape, while young, post-harvest stands will increase in abundance. To determine the effects this harvesting strategy might have on communities of breeding forest birds, we conducted point counts in young forests regenerated from clear-cutting (15–25 years), and mature (50–60 years), and old (80–110 years) forests regenerated from fire. Avian species richness was highest in old stands at the point-count station, forest stand, and landscape level. Increased species richness with forest age was associated with increases in the relative abundance of canopy- and cavity-nesting species. At local scales (station and stand), species richness of ground- and shrub-nesting birds was similar among forest age-classes. However, as determined by rarefaction analyses appropriate at the landscape scale, ground-nesting species were more common in young and old forests, while shrub-nesting species were more common in young and mature forests. Density of deciduous shrubs was an important factor influencing the abundance of species like American redstart, Canada warbler, and chestnut-sided warbler. An increase in conifer in old stands resulted in greater use by conifer- or mixedwood associated species such as bay-breasted warbler, magnolia warbler, and ruby-crowned kinglet. Our data indicate that vegetation and structural characteristics such as shrub density should be considered when prescribing sustainable forestry objectives. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Concern that increasing timber harvest in the boreal mixedwood zone of western Canada (Peterson and Peterson, 1992; Cummings et al., 1994; Stelfox, 1995) will negatively influence the region's avian communities has resulted in several recent investigations, especially in Alberta (Schmiegelow and Hannon,

1993; Schieck et al., 1995; Schmiegelow et al., 1997). New forest licence agreements in Alberta, Saskatchewan, and Manitoba have targeted much of the mature and old aspen in the Canadian prairies for harvesting within the next 20 years. Regeneration plans for this region are designed to use a rotation system with a harvest interval of less than 70 years (Weyerhaeuser Canada, 1998). Although timber harvest can influence bird communities in several ways (Welsh, 1987), a current issue is the possibility that short cutting rotations will truncate natural age distributions and reduce habitat for those species

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requiring older stands (Flack, 1976; Schieck et al., 1995; Kirk et al., 1996). In addition, it is currently not clear how closely post-harvest stands resemble post-fire stands in terms of their suitability as avian habitat (but see Hobson and Schieck, 1999) and these younger post-harvest stands are expected to increase in abundance. To implement sustainable forest management (Walters, 1986; Hunter, 1990), it is important to identify those bird species negatively affected by changes in stand age-class distributions and stand type over the landscape and determine whether such patterns are consistent across regions (Schieck et al., 1995; Welsh and Lougheed, 1996; Thingstad, 1997).

Whether mature aspen stands have the necessary attributes to support older-growth bird communities, if these exist, is unclear. Previous studies have suggested that old aspen forests have a greater variety of resources for birds, particularly those that nest in the canopy or in cavities, due to the larger size of canopy trees, and the higher density of standing dead trees (Flack, 1976; Erskine, 1977). For example, Schieck et al. (1995), in their study of bird communities associated with three age-classes of fire-origin aspen-dominated stands in east–central Alberta, found that species richness was highest in old aspen stands, intermediate in young stands, and lowest in mature stands. In contrast, Westworth and Telfer (1993) found that species richness in western Alberta was highest in 14 year old stands and that the abundance of cavity-nesting species was similar regardless of forest age. It is possible then, that regional differences in avian community response to stand age and/or structure of aspen-dominated stands occurs or, alternatively, that stand age and tree composition per se, may not alone be reliable predictors of avian community composition. This creates a dilemma for managers who may wish to rely primarily on forest inventory data to predict habitat supply for bird communities.

The objectives of this study were to compare avian communities in young (15–25 years), mature (50–60 years), and old aspen forest (80–110 years) in central Saskatchewan. We were interested in knowing: (a) how stand age influenced the structure of bird communities; and (b) what forest attributes influenced the occurrence of species in different aged forests. We extend the earlier investigation of Schieck et al. (1995) by considering young stands following harvest rather than fire because these are the stand types that will largely replace fire-origin forests in our study area in the near future.

2. Methods

Our study was conducted within the southern boreal ecoregion of Saskatchewan (Kabzems et al., 1986). Surveys were conducted in and around the Prince Albert Model Forest (Bouman et al., 1996) located about 70 km north of Prince Albert, Saskatchewan (53°50′N; 105°50′W) during the summers of 1993 and 1994. Initial site selection was based on provincial forest inventory maps and cover maps for Prince Albert National Park. To avoid landscape influences such as edge that can influence breeding bird communities (Gates and Gysel, 1978), we chose stands that were located in contiguous forest and were bordered only by an access road or trail. Generally, five or six survey stations were located within a single forest stand, with the requirement that these stations were at least 250 m apart and 100 m from an edge, including edges of other stand types. Occasionally, we were only able to fit four stations within a stand. On average, stands were about 25 ha in size. We conducted surveys at 29 stations (6 sites) in young, 39 stations (8 sites) in mature, and 37 stations (7 sites) in old forests. Each survey point was sampled in only 1 year. All young stands had regenerated following clear-cutting without the maintenance of standing residual live trees, while all mature and old forests had regenerated following natural fire. Sites were distributed throughout an area of approximately 400,000 ha and were a minimum of 3 km apart.

2.1. Vegetation survey techniques

At each bird survey station, vegetation characteristics were recorded in four 0.04 ha (11.3 m radius) circles situated 25 m from the station in each of the four cardinal directions (James and Shugart, 1970). In each circle, the number of trees of each species were recorded and were categorized as either canopy or subcanopy trees. In the same circle, we also counted the number of coniferous and deciduous standing snags. Tree height and diameter-at-breast-height (DBH) were measured for two individuals of each tree species using a modified point-quarter method.

The first tree measured was nearest to the centre of the sampling circle, while the second tree was the next nearest neighbour of the same species. Along a 22.6 m transect line through the centre of each circle, we recorded the number of fallen woody stems of five different diameter classes (<5, 5–10, 10–20, 20–30, and >30 cm) that intersected the transect.

Within each circle, two 16 m^2 sub-plots were placed at each end of the 22.6 m transect line. Within each sub-plot, we established four cells of 4 m^2 each. In the first cell on the right side of the transect, the stem density of each species of shrub over 1 m in height was counted. In the other cells, shrub density was counted or estimated based on the results of the first cell count. The average shrub height in all cells was then estimated for each species. In the first cell, percent cover of low shrub, moss, grass, and herb were estimated to the nearest 10%.

Vegetation data were summarized into 16 variables (Table 1): (1) density of deciduous trees (stems/ha); (2) % of deciduous trees in canopy; (3) density of coniferous trees in canopy (stems/ha); (4) % of coniferous trees in canopy (stems/ha); (5) density of snags (stems/ha); (6) tree species richness; (7) average canopy height (m); (8) density of deciduous shrubs (stems per 25 m^2); (9) density of coniferous shrubs (stems per 25 m^2); (10) shrub species richness; (11) shrub height (m); (12) % grass cover; (13) % herb cover; (14) % low shrub cover; (15) % moss cover; and (16) volume (m^3/ha) of dead woody material (DWM). Volume of DWM was calculated using Van Wagner (1968) formula

$$V = \left(\frac{1000\,\pi^2}{8l}\right) \sum d_{I^2}$$

where V is the volume of DWM (m^3/ha), l is the length of the transect (m), and d_I is the diameter (m) of the Ith piece of DWM on the transect. Diameter-at-breast-height was excluded from our analysis due to the strong correlation with tree height ($r = 0.78$).

2.2. Avifauna survey techniques

Breeding bird surveys were conducted twice at each site, once in early June and once in late June (the only month when territorial males sing regularly at this latitude). Surveys involved early-morning point counts (04:00–09:00 hours) at each station within

Table 1
Mean (±1 SE) differences in vegetation attributes per station among young, mature, and old aspen forests. Also included are results of single-factor Kruskal–Wallis tests examining differences between stand ages

Vegetation attributes	Young	Mature	Old	H	P
No. of stations	29	39	37	–	–
No. of sites	6	8	7	–	–
Age (years)	21 ± 1 (15–25)[a]	54 ± 1 (50–60)	90 ± 2 (80–110)	–	–
Density deciduous trees (stems/ha)	2327 ± 144	688 ± 66	335 ± 40	68.4	0.001
% Deciduous trees in canopy (stems/ha)	62 ± 3	72 ± 4	65 ± 6	7.2	0.02
Density coniferous trees (stems/ha)	209 ± 34	40 ± 15	71 ± 20	29.8	0.001
% Coniferous trees in canopy (stems/ha)	7 ± 3	21 ± 6	7 ± 2	0.6	0.72
Tree species richness	5.0 ± 0.3	3.1 ± 0.3	2.9 ± 0.2	32.2	0.001
Average canopy height (m)	11.8 ± 0.4	17.3 ± 0.4	22.8 ± 0.4	82.8	0.001
Density snags (stems/ha)	209 ± 26	319 ± 28	310 ± 36	10.2	0.006
Volume of DWM (m^3/ha)	68 ± 13	82 ± 9	110 ± 10	10.2	0.006
Density deciduous shrubs (stems/25 m^2)	83 ± 20	143 ± 27	61 ± 14	13.4	0.001
Density coniferous shrubs (stems/25 m^2)	3 ± 1	1 ± 1	4 ± 1	16.1	0.001
Shrub species richness	5.9 ± 0.6	4.8 ± 0.6	5.2 ± 0.5	1.9	0.37
Shrub height	1.3 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	21.8	0.001
% Grass cover	20 ± 3	21 ± 4	17 ± 3	0.3	0.86
% Herb cover	47 ± 3	50 ± 4	44 ± 3	1.8	0.42
% Low shrub cover	30 ± 4	36 ± 3	27 ± 3	5.5	0.07
% Moss cover	7 ± 1	8 ± 2	18 ± 4	5.7	0.05

[a] Age range of stations surveyed.

each site based on the Indice Ponctual D'Abondance technique of Blondel et al. (1970). At each survey station, all birds heard or seen during a 10 min count period were recorded. Counts were of unlimited distance, subject to the constraint that only birds estimated to be within the stand were recorded. Data mapping forms used were similar to those included in Ralph et al. (1992). Observers recorded the approximate location of singing birds on these maps and excluded those birds that they believed were detected previously. Surveys were performed by four experienced observers over the 2 years of the study. Observers were tested in the lab and field to ensure similar levels of expertise. However, to reduce the influence of observer bias, each observer surveyed each station only once and the order of site visits was chosen randomly. All bird species believed to have nested or foraged within the sampled sites were treated as members of the forest bird community. We excluded those species that typically nest in wetland habitats (e.g., red-winged blackbird, *Agelaius phoeniceus*) or whose foraging territories were much larger than the forests in which they were detected (e.g., raptors). To determine if avian community structure was influenced by forest age, we placed species into nesting guilds (i.e. ground, shrub, canopy and cavity nesters: see Table 2). Nesting guild was determined from the literature (primarily Schieck et al., 1995) and our own observations.

2.3. Statistical analyses

Differences in vegetation structure among the forest age-classes were determined using a series of Kruskal–Wallis tests. A discriminant function analysis was also used to determine if overall vegetation structure differed among forest age-classes.

Avian species richness was calculated for each station and for all point count stations within a site. To determine if species richness was significantly different among forest age classes, we conducted a series of single-factor analysis of variance (ANOVA) tests. When the ANOVA was significant ($P = 0.05$), we used a Tukey's highly significant difference (HSD) test to determine which forest age categories were different for that variable. We also estimated species richness at the landscape scale using rarefaction analyses based on the number of species per 25 stations.

Rarefaction is a statistical method that estimates the number of species expected from a given sample of point counts based on multiple random sampling (James and Rathbun, 1981). Rarefaction estimates were calculated using the computer program EstimateS 5 (Colwell, 1987). Differences in landscape richness between age-classes were determined by using the mean species richness per 25 stations and standard deviation estimates to calculate a single factor ANOVA. We also used a series of non-parametric Kruskal–Wallis tests to determine if there was a significant difference in the relative abundance of individual species in each forest age class. Contingency table analyses were used to determine if the probability of occurrence of each species was different between forest age-classes. For individual species, data were also analyzed at both the site and station level.

To determine which vegetation attributes influenced the abundance of individual bird species, we conducted a detrended correspondence analysis (DCA) using the computer program PC-Ord (McCune and Mefford, 1997). DCA is an ordination technique that groups species in a two-dimensional scatterplot. In a DCA scatterplot, species with similar habitat requirements are close to one another, whereas sites closer together have similar avian communities. To determine which vegetation characteristics were related to variation in bird communities, we included the vegetation variables as a passive environmental data set in the DCA analysis and calculated Pearson correlation coefficients between each vegetation variable and the site scores on the DCA axes (ter Braak, 1992). Species-environmental biplots (ter Braak, 1992) were prepared that showed how each species was related to the most important vegetation variables. The length of the arrow in the biplot indicates the strength of the correlation between that environmental variable and the DCA function. The direction of the arrow indicates how a particular vegetation variable was related to bird-abundance in two-dimensional DCA space. Canonical correspondence analysis (CCA) was not used for this analysis because we wanted to highlight the variation that existed in the avian community and much of this variation is ignored in CCA if important vegetation characteristics are not included in the analysis (Halvorsen, 1996). All bird densities and vegetation attributes were log transformed prior to

Table 2
Mean (±1 SD) abundance and results of single factor Kruskal–Wallis tests of each bird species per station in each age class. The % of stations where each species was detected is also given, along with the results of a likelihood ratio test

AOU code	Common name	Species name	Relative abundance				% Stations detected			
			Young	Mature	Old	P	Young	Mature	Old	P
Ground nesters			5.75 ± 0.40	7.64 ± 0.42	6.83 ± 0.48	0.02	–	–	–	–
BWWA	Black-and-white warbler	*Mniotilta varia*	0.14 ± 0.35	0 ± 0	0.14 ± 0.35	0.05	13.8	0	15.6	0.01
CAWA	Canada Warbler	*Wilsonia canadensis*	0.1 ± 0.31	0.18 ± 0.45	0.05 ± 0.23	0.36	11.6	15.4	5.7	0.35
COWA	Connecticut Warbler	*Oporornis agilis*	0.38 ± 0.62	0.49 ± 0.76	0.3 ± 0.7	0.30	31.0	35.9	18.9	0.23
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	0 ± 0	0.03 ± 0.16	0 ± 0	0.43	0	2.6	0	0.37
MOWA	Mourning Warbler	*Oporornis philadelphia*	0.14 ± 0.35	0.33 ± 0.58	0.16 ± 0.44	0.18	13.8	28.2	13.5	0.19
NAWA	Nashville Warbler	*Vermivora ruficapilla*	0.03 ± 0.19	0 ± 0	0.03 ± 0.16	0.54	3.4	0	2.7	0.53
OCWA	Orange-crown. Warbler	*Vermivora celata*	0.03 ± 0.19	0.03 ± 0.16	0.03 ± 0.16	0.97	3.4	2.6	2.7	0.98
OVEN	Ovenbird	*Seiurus aurocapillus*	2.38 ± 1.27	3.79 ± 1.34	2.89 ± 1.2	0.001	93.1	100	100	0.07
RUGR	Ruffed Grouse	*Bonasa umbellus*	0.21 ± 0.49	0.15 ± 0.43	0.3 ± 0.62	0.56	17.2	12.8	21.6	0.60
SWSP	Swamp Sparrow	*Melospiza georgiana*	0.03 ± 0.19	0 ± 0	0 ± 0	0.27	3.4	0	0	0.27
SWTH	Swainson's Thrush	*Catharus ustulatus*	0.14 ± 0.35	0.44 ± 0.75	0.54 ± 0.93	0.14	13.8	30.8	32.4	0.15
TEWA	Tennessee Warbler	*Vermivora peregrina*	0.83 ± 1.04	0.79 ± 1	1.38 ± 1.34	0.12	51.7	48.7	59.5	0.63
WIWA	Wilson's Warbler	*Wilsonia pusilla*	0.07 ± 0.26	0 ± 0	0.05 ± 0.23	0.28	6.9	0	5.4	0.28
WTSP	White-throated Sparrow	*Zonotrichia albicolis*	1.17 ± 1.36	1.33 ± 0.96	0.89 ± 0.88	0.10	65.5	82.1	64.9	0.17
Shrub nesters			4.72 ± 0.54	6.31 ± 0.52	5.13 ± 0.47	0.10	–	–	–	–
ALFL	Alder Flycatcher	*Empidonax minimus*	0.07 ± 0.26	0.08 ± 0.35	0.05 ± 0.33	0.75	6.8	5.1	2.7	0.72
AMGO	American Goldfinch	*Carduelis tristis*	0.07 ± 0.26	0.03 ± 0.16	0.03 ± 0.16	0.60	6.9	2.6	2.7	0.59
AMRE	American Redstart	*Setophaga ruticilla*	0.62 ± 1.05	1.38 ± 1.9	0.76 ± 1.46	0.18	34.5	48.7	35.1	0.37
AMRO	American Robin	*Turdus migratorius*	0 ± 0	0.15 ± 0.43	0 ± 0	0.01	0	12.8	0	0.01
BLJA	Blue Jay	*Cyanocitta cristata*	0 ± 0	0.03 ± 0.16	0 ± 0	0.43	0	2.6	0	0.42
CCSP	Clay-coloured Sparrow	*Spizella pallida*	0.03 ± 0.19	0 ± 0	0 ± 0	0.27	3.4	0	0	0.27
CHSP	Chipping Sparrow	*Spizella passerina*	0.24 ± 0.51	0.28 ± 0.51	0.24 ± 0.43	0.91	20.7	25.6	24.3	0.89
CSWA	Chestnut-sided Warbler	*Dendroica pensylvanica*	0.59 ± 1.09	0.64 ± 0.9	0.24 ± 0.64	0.03	31.0	43.6	13.5	0.01
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	0.1 ± 0.41	0.31 ± 1.06	0.08 ± 0.28	0.63	6.9	12.8	8.1	0.67
HETH	Hermit Thrush	*Catharus guttatus*	0.62 ± 0.82	0.44 ± 0.72	0.76 ± 1.04	0.45	44.8	33.3	40.5	0.61
MAWA	Magnolia Warbler	*Dendroica magnolia*	0.03 ± 0.19	0.15 ± 0.43	0.41 ± 0.76	0.01	3.4	12.8	29.7	0.01
MODO	Mourning Dove	*Zenaida macroura*	0.14 ± 0.35	0.03 ± 0.16	0 ± 0	0.02	13.8	2.6	0	0.02
NOOR	Northern Oriole	*Icterus galbula*	0.03 ± 0.19	0 ± 0	0 ± 0	0.27	3.4	0	0	0.27
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	0.31 ± 0.54	0.36 ± 0.71	0.22 ± 0.58	0.54	27.6	23.1	16.2	0.52
REVI	Red-eyed Vireo	*Vireo olivaceus*	1.62 ± 1.12	1.87 ± 1.17	1.68 ± 1.16	0.64	82.8	87.2	83.8	0.86
SOVI	Solitary Vireo	*Vireo solitarius*	0 ± 0	0.03 ± 0.16	0.11 ± 0.39	0.20	0	2.6	8.1	0.20
WIWR	Winter Wren	*Troglodytes troglodytes*	0 ± 0	0 ± 0	0.05 ± 0.23	0.15	0	0	5.4	0.12
WWPE	Western Wood-Peewee	*Contopus sordidulus*	0.03 ± 0.19	0 ± 0	0 ± 0	0.56	3.4	2.6	0	0.41
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	0.17 ± 0.47	0.31 ± 0.52	0.32 ± 0.58	0.36	13.8	28.2	27.0	0.30

Table 2 (*Continued*)

AOU code	Common name	Species name	Relative abundance				% Stations detected			
			Young	Mature	Old	*P*	Young	Mature	Old	*P*
Canopy nesters			0.79 ± 0.17	1.28 ± 0.19	1.59 ± 0.26	0.07	–	–	–	–
AMCR	American Crow	*Corvus brachyrhynchos*	0 ± 0	0.05 ± 0.22	0 ± 0	0.18	0	5.4	0	0.18
BBWA	Bay-breasted Warbler	*Dendroica castanea*	0 ± 0	0 ± 0	0.19 ± 0.4	0.001	0	0	18.9	0.001
BLWA	Blackburnian Warbler	*Dendroica fusca*	0 ± 0	0 ± 0	0.03 ± 0.16	0.40	0	0	2.7	0.40
BTNW	Black-thr. Green Warbler	*Dendroica virens*	0.03 ± 0.19	0.1 ± 0.31	0.03 ± 0.16	0.31	3.4	10.2	2.7	0.30
CEWX	Cedar Waxwing	*Bombycilla cedrorum*	0.07 ± 0.37	0.26 ± 0.64	0.24 ± 0.76	0.21	3.4	17.9	13.5	0.19
CMWA	Cape May Warbler	*Dendroica tigrina*	0.03 ± 0.19	0 ± 0	0.03 ± 0.16	0.54	3.4	0	2.7	0.38
CORA	Common Raven	*Corvus corax*	0.38 ± 0.62	0.15 ± 0.37	0.27 ± 0.56	0.27	31.0	15.4	21.6	0.31
GRJA	Gray Jay	*Perisoreus canadensis*	0.03 ± 0.19	0.13 ± 0.52	0.16 ± 0.44	0.34	3.4	7.7	13.5	0.32
LEFL	Least Flycatcher	*Empidonax minimus*	0.14 ± 0.44	0.28 ± 0.6	0.11 ± 0.66	0.05	10.3	20.5	2.7	0.04
PHVI	Philadelphia Vireo	*Vireo philadelphicus*	0.03 ± 0.19	0.13 ± 0.34	0 ± 0	0.05	3.4	12.8	0	0.02
PISI	Pine Siskin	*Carduelis pinus*	0.07 ± 0.26	0.15 ± 0.43	0.41 ± 0.69	0.02	6.9	12.8	32.4	0.02
PUFI	Purple Finch	*Carpodacus purpureus*	0 ± 0	0.03 ± 0.16	0 ± 0	0.43	0	2.6	0	0.37
RCKI	Ruby-crowned Kinglet	*Regulis calendula*	0.03 ± 0.19	0.21 ± 0.52	0.19 ± 0.46	0.22	3.4	15.4	16.2	0.16
WWCR	White-winged Crossbill	*Loxia leucoptera*	0 ± 0	0 ± 0	0.14 ± 0.42	0.02	0	0	10.8	0.01
Cavity nesters			0.45 ± 0.14	0.41 ± 0.13	1.46 ± 0.30	0.001	–	–	–	–
BCCH	Black-capped Chickadee	*Parus atricapillus*	0 ± 0	0 ± 0	0.3 ± 1.02	0.003	0	0	16.2	0.002
BOCH	Boreal Chickadee	*Parus hudsonicus*	0 ± 0	0 ± 0	0.03 ± 0.16	0.40	0	0	2.7	0.40
BRCR	Brown Creeper	*Certhia americana*	0 ± 0	0.03 ± 0.16	0.22 ± 0.48	0.005	0	2.6	18.9	0.05
HAWO	Hairy Woodpecker	*Picoides villosus*	0.03 ± 0.19	0.05 ± 0.22	0.08 ± 0.28	0.71	3.4	5.1	8.1	0.71
NOFL	Northern Flicker	*Colaptes auratus*	0.03 ± 0.19	0.03 ± 0.16	0.11 ± 0.31	0.25	3.4	2.6	10.8	0.26
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	0 ± 0	0.1 ± 0.38	0.19 ± 0.4	0.03	0	7.7	18.9	0.01
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	0.14 ± 0.35	0.05 ± 0.22	0.41 ± 0.55	0.001	13.8	5.0	37.8	0.001
WBNU	White-breasted Nuthatch	*Sitta carolinesis*	0.03 ± 0.19	0.08 ± 0.35	0.05 ± 0.23	0.92	3.4	5.1	5.4	0.92
YBSA	Yellow-bel. Sapsucker	*Sphyrapicus varius*	0.21 ± 0.49	0.08 ± 0.27	0.08 ± 0.28	0.36	17.2	7.7	8.1	0.40
Other										
BHCO	Brown-headed Cowbird	*Molothrus ater*	0.03 ± 0.19	0.08 ± 0.27	0.08 ± 0.28	0.72	3.5	7.7	8.1	0.7

analysis except for % cover estimates which were arcsine transformed. AOU reference codes and Latin names for all birds species are given in Table 2.

3. Results

3.1. Vegetation

Eleven of the 16 vegetation characteristics measured, differed significantly among age-classes. Density of deciduous trees, canopy height, volume of DWM, density of snags, and % moss cover all increased with forest age (Table 1). A larger proportion of the trees were in the canopy in mature stands than in young or old stands. Density of deciduous shrubs was highest in mature forest, intermediate in young, and lowest in old stands of aspen. Density of coniferous shrubs and trees was highest in young stands, lowest in mature, and intermediate in old stands. Finally, tree species richness declined with forest age. All other vegetation variables showed no differences among forest age-classes.

Discriminant function analysis correctly classified 94.3% of all point-count stations into the apriori forest age-classes ($F = 42.0$, $P < 0.001$; Fig. 1). The first canonical discriminant function accounted for 93.3% in the vegetation data, and was correlated with deciduous tree density ($r = 0.30$), and negatively correlated with canopy height ($r = -0.68$) and DWM ($r = -0.12$). The second function was positively correlated with deciduous shrub density ($r = 0.46$), shrub height ($r = 0.38$), low shrub cover ($r = 0.27$), and snag density ($r = 0.19$). In addition, the second function was negatively correlated with coniferous shrub density ($r = -0.44$), coniferous tree density ($r = -0.43$), moss cover ($r = -0.23$), and tree species richness ($r = -0.22$).

3.2. Avifauna

We detected a total of 1505 individuals of 56 species in all age-classes of forests combined (Table 2). Many species were rare, with 18 species detected at less than five stations. Species richness at the station level was significantly higher in old and mature forest than it was in young forest (Table 3). A similar pattern was observed at the site level, although this was not statistically significant due to low statistical power. At the landscape level (i.e., based on rarefaction analyses), we found a similar pattern with old forests having higher species richness than young or mature forest (Table 3 and Fig. 2A).

Guild structure of the avian community was highly influenced by forest age. More species nested in the canopy (e.g., bay-breasted warbler, purple finch, pine siskin) in mature, and old forests than in young stands (Table 3). Similarly, cavity-nesting species (e.g. black-capped chickadee, pileated woodpeckers, red-breasted nuthatch and brown creeper) were more common in old stands than in either young or mature stands (Table 3). Species abundance for the other nesting guilds were not significantly influenced by forest age at station or site scales (Table 3). Patterns of species richness observed for cavity- and canopy-nesters at the landscape scale were similar to those found at the station and site scale (Table 3 and Fig. 2D and E). However, at the landscape scale, the number of ground-nesting species was highest in young, intermediate in old, and lowest in mature forest (Table 3 and Fig. 2B). Conversely, more shrub-nesting species were found in young and mature stands at the landscape level than in old stands (Table 3 and Fig. 2C).

At the station level, 15 species had significantly different relative abundance and probability of occurrence in a particular age-class (Table 2). These differences were mainly dependent on nesting guild. Of the 14 ground-nesting species we identified, only the ovenbird showed a significant difference in relative abundance among age-classes, reaching its highest abundance in mature stands. For the 19 shrub-nesting
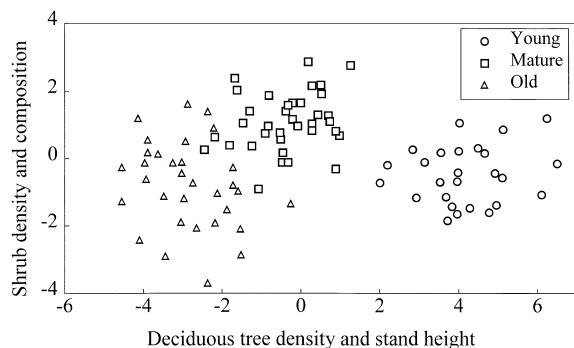

Fig. 1. Scatterplot depicting results of discriminant function analysis for vegetation attributes in each forest age class. Points closer together have greater similarity in vegetation characteristics.
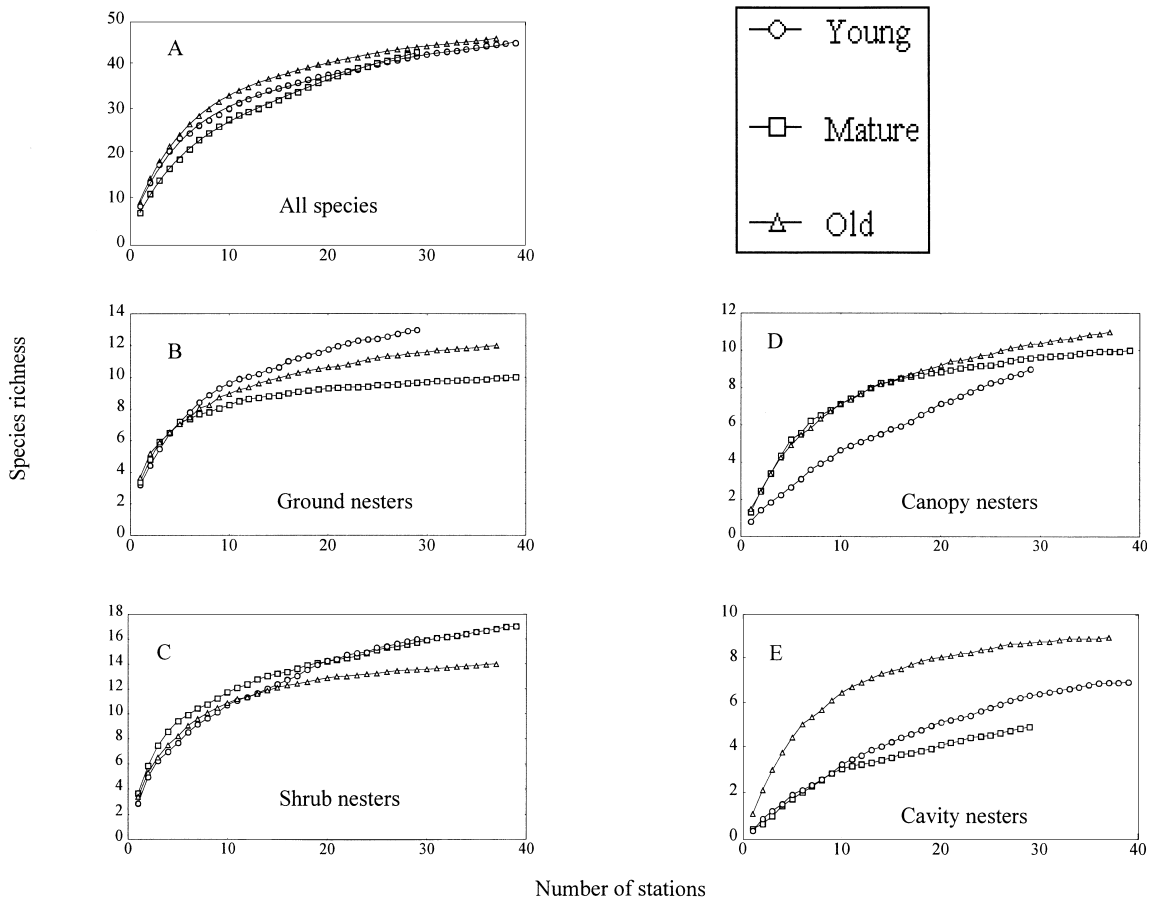
Fig. 2. Rarefaction curves showing the mean species richness detected at various numbers of point count stations in young, mature, and old aspen forest, for: (A) all bird species; (B) ground-nesting species; (C) shrub-nesting species; (D) canopy-nesting species; (E) cavity-nesting species.

species, American robin, chestnut-sided warbler, and mourning dove had significantly higher relative abundance and were most common in young and mature forests. Conversely, magnolia warbler reached highest abundance in old stands. Canopy-nesting species were more likely to be affected by forest age and, of these, blackburnian warbler, pine siskin, and white-winged crossbill had significantly higher abundance in old stands. Similarly, Philadelphia vireo was more likely to be found in mature stands than in young stands, although it was not detected in old stands. Of the nine cavity-nesting species, all but two had their highest abundance in old stands, with black-capped chickadee, brown creeper, pileated woodpecker, and red-

breasted nuthatch showing statistically significant differences.

Very few species showed a preference for a particular age class when we used stand-level data. This was not unexpected due to low statistical power for most of these tests. However, the forest age-class having the highest abundance of a particular species at the station level was also the same age-class with the highest abundance at the site level. This pattern occurred for all species except red-eyed vireo, which showed no difference in abundance at either scale.

As ordination techniques are highly influenced by rare species (ter Braak, 1992), we used only those 39 species detected at a minimum of 5 stations when constructing our ordination. The first DCA function

Table 3
Mean (±1 SD) number of species in each nesting guild detected at the station, site, and landscape scales in each forest age class. Also given are the results of single-factor ANOVA tests. Those age-classes sharing a letter are not significantly different from one another based on a Tukey's HSD test

Scale	Young	Mature	Old	F	P
All species					
Station	7.4 ± 2.2	8.7 ± 2.3	9.1 ± 2.8	7.4	0.03
Site	15.8 ± 3.1	18.5 ± 3.3	20.0 ± 4.1	2.3	0.13
Landscape	40.6 ± 1.6	40.3 ± 1.8	42.7 ± 1.3	17.1	0.001
Ground nesters					
Station	3.3 ± 1.2	3.6 ± 1.4	3.4 ± 1.6	0.42	0.66
Site	6.2 ± 1.6	6.1 ± 1.7	5.4 ± 1.7	0.41	0.66
Landscape	12.4 ± 0.7	9.5 ± 0.7	11.2 ± 0.7	108.3	0.001
Shrub nesters					
Station	3.1 ± 1.6	3.6 ± 1.3	3.1 ± 1.4	1.6	0.20
Site	6.7 ± 2.3	7.0 ± 1.3	6.7 ± 1.8	0.7	0.93
Landscape	15.1 ± 1.3	15.3 ± 0.7	13.2 ± 0.6	39.7	0.001
Canopy nesters					
Station	0.6 ± 0.7	1.1 ± 0.9	1.2 ± 1.1	3.3	0.04
Site	2.0 ± 0.9	3.6 ± 0.7	3.6 ± 1.7	3.9	0.04
Landscape	8.2 ± 0.7	8.2 ± 0.7	9.8 ± 0.9	35.7	0.001
Cavity nesters					
Station	0.4 ± 0.6	0.4 ± 0.6	1.3 ± 1.2	12.8	0.001
Site	1.0 ± 0.6	1.3 ± 1.2	4.1 ± 2.0	10.4	0.001
Landscape	4.6 ± 0.5	6.0 ± 0.9	8.5 ± 0.6	206.1	0.001

Table 4
Pearson correlation coefficients (r) for 17 vegetation variables with first two DCA functions. Also reported is the significance value of each correlation

Vegetation variables	Function 1		Function 2	
	DCA	P	DCA	P
Age (years)	0.31	0.001	0.11	0.26
Density deciduous trees (stems/ha)	−0.42	0.001	0.17	0.08
% Deciduous trees in canopy (stems/ha)	−0.1	0.29	0.11	0.26
Density coniferous trees (stems/ha)	0.26	0.01	−0.04	0.67
% Coniferous trees in canopy (stems/ha)	0.13	0.18	0	0.97
Tree species richness	−0.05	0.59	0.05	0.62
Average canopy height (m)	0.22	0.03	0.09	0.37
Density snags (stems/ha)	0.26	0.01	−0.21	0.03
Volume of DWM (m/ha)	−0.01	0.94	0	0.97
Density deciduous shrubs (stems/25 m)	−0.75	0.001	0.08	0.39
Density coniferous shrubs (stems/25 m)	0.58	0.001	−0.13	0.18
Shrub species richness	0.13	0.18	0.12	0.23
Shrub height	0.02	0.82	−0.22	0.02
% Grass cover	−0.2	0.04	0.36	0.001
% Herb cover	0.15	0.12	0.16	0.11
% Low shrub cover	−0.25	0.01	0.08	0.42
% Moss cover	0.55	0.001	0.08	0.42

explained 11.1% of the variation in the species data (Eigenvalue = 0.37: Fig. 3A and B). This function was significantly correlated with the density of coniferous shrubs, % moss cover, stand age, density of coniferous trees, snag density, and tree height (Table 4). Conversely, this axis was negatively correlated with density of deciduous shrubs, density of

deciduous trees, and % cover of low shrubs. Function 2 accounted for 5.7% (Eigenvalue = 0.189) of the variance in the bird data set. This function was correlated with % grass cover and negatively correlated with shrub height and snag density.

Shrub density was the major factor influencing the avian community in aspen forests in our study area
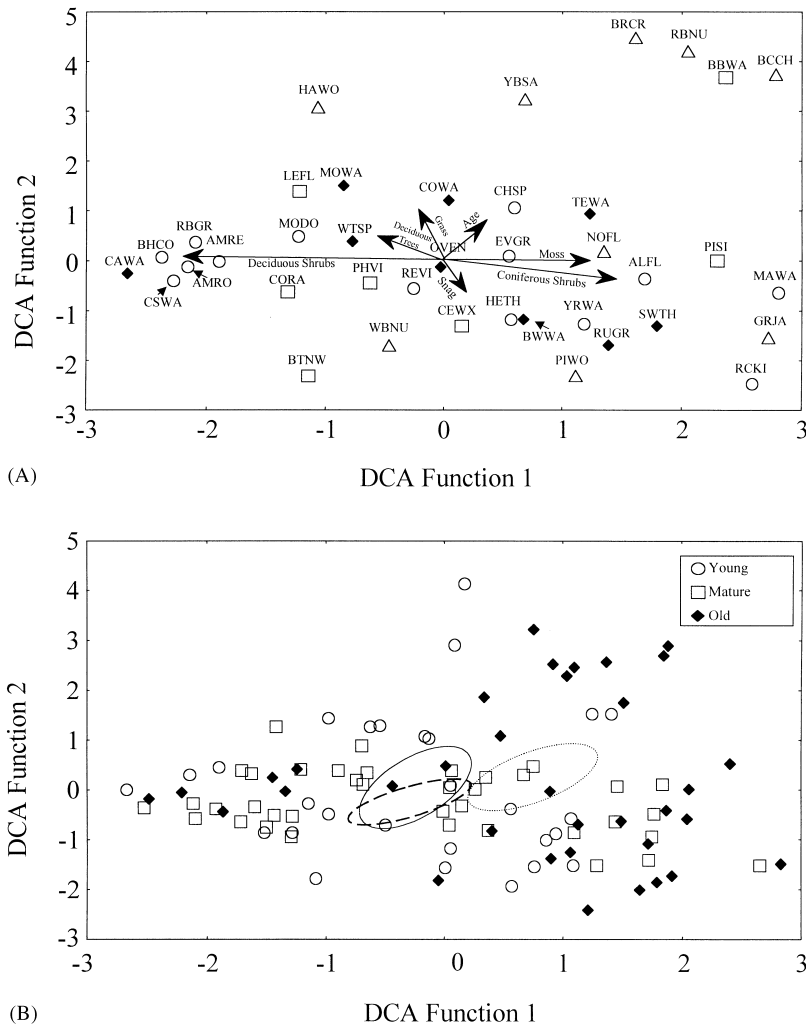
Fig. 3. (A) Scatterplot depicting results of a detrended correspondence analysis (DCA) at the species level. AOU codes for each species are given in Table 2. Species closer together have greater similarity in their habitat requirements than those that are farther apart. Arrows represent the strength and direction of the correlation between the environmental variables and a particular DCA axis. Different symbols are used to indicate the nesting strata used by a particular species. (B) Location of each point count station in multivariate space. Points closer to one another have greater similarity in the avian community than those that are further apart. Ellipses represent 95% confidence interval around the centroid for each age class. The solid ellipse is for young aspen, the thick-dashed ellipse for mature aspen, and the thin-dashed ellipse for old aspen stands.

(Fig. 3A). Those species found on the left side of the ordination were strongly associated with forests that had high densities of deciduous shrubs which included mainly mature, but also some young and old forests. In particular, the American redstart, American robin, chestnut-sided warbler, Canada warbler, and rose-breasted grosbeak were most likely to be found in forests with high deciduous shrub cover. The shrub species that dominated in these sites was beaked hazelnut (*Corylus cornuta*). In contrast, those species on the right side of the ordination (Fig. 3A) were most commonly associated with old stands (Fig. 3B). In particular, these species seemed to respond to an increased conifer component, both at the shrub level and in the canopy. Of the 11 ground- and shrub-nesting species found on the right side of the ordination, 9 are most commonly associated with conifer-dominated forests (Schieck et al., 1995; Kirk et al., 1996). Most (5 of 7) of the species nesting in the canopy were found in the centre of the ordination, suggesting that they were present in a wide variety of forest age-classes, although many were most abundant in old forest. Bay-breasted warbler and pine siskin were two canopy species having a strong affiliation for old forests, in part likely due to the higher number of coniferous trees in that age class. As expected, the majority (7 of 9) of the cavity-nesting species were on the right side of the ordination indicating a preference for old forest. Hairy woodpecker and white-breasted nuthatch were the exceptions to this pattern, but both of these species were detected relatively infrequently. Very similar patterns were observed when data were analyzed at the site level and are not presented.

4. Discussion

The distinct changes in floristic composition and structure observed in western boreal aspen forests with increasing age (Westworth and Telfer, 1993; Schieck et al., 1995) influences the number and type of niches available for breeding birds (James and Wamer, 1982; Moskat and Szekely, 1989). In aspen forests of Saskatchewan, we found that old forests had higher species richness than mature or young stands. The strength of this effect differed according to nesting guild and the scale at which species richness was measured. Overall, increased species richness in old stands was caused by increases in the number of cavity-nesting species, and to a lesser extent increases in the number of canopy-nesting species.

Several factors may have influenced the higher abundance of cavity-nesting species we recorded in our old forests. Like Schieck et al. (1995), we found that as aspen forests age, a decrease in deciduous tree density occurs during which canopy height, tree DBH, and volume of DWM increase (Lee et al., 1997). Given the importance of snags to cavity nesting birds (Flack, 1976; Francis and Lumbis, 1979; Peterson and Peterson, 1992; Schieck et al., 1995), we expected that old stands would have greater number of standing snags but we did not find such a pattern. However, Flack (1976) demonstrated that use of aspen forest by woodpeckers depended not just on the availability of snags, but also on the size of those snags, with most woodpeckers requiring snags with a DBH greater than 15 cm. Thus, the number of large snags may be a better predictor of the presence of cavity-nesting species rather than snag density per se. Alternatively, as found in several previous studies, size and distribution of live trees may have been more important to cavity-nesting species than the presence of snags alone (Land et al., 1989; Lundquist and Mariani, 1991; Welsh and Capen, 1992; James et al., 1997). We found that cavity nesting species were relatively uncommon in our young stands relative to similar aged stands in Alberta that had residual trees leftover from the previous fire (Westworth and Telfer, 1993). Residual trees were rare in our young stands, as all our stands were regenerated from clear-cutting and little standing material was left on site. This may have prevented some cavity nesting species from using our young stands such as the northern flicker that are known to use young stands with residual trees (Kirk et al., 1996).

Although the occurrence of cavity-nesting species was the main factor influencing the relationship between species richness and stand age in our study, another important variable was the change in the coniferous tree component with stand age. Changes in vegetation structure due to the presence of conifers has been shown to have important effects on bird communities in many areas of North America (Willson, 1974; Collins et al., 1982; James and Wamer, 1982; Willson and Comet, 1996). In our study, con-

iferous trees occurred in all forest age-classes but their contribution to overall stand structure was higher in old stands (18%) than in young (8%) or mature forests (5%). Canopy nesting birds like bay-breasted warbler, grey jay, magnolia warbler, pine siskin, and ruby-crowned kinglet all tended to occur in old stands that had higher densities of coniferous trees and shrubs. These species are often more strongly associated with deciduous-conifer mixedwoods or conifer-dominated stands rather than aspen stands per se (Kirk et al., 1996). Thus, the effective management of these birds will also be linked to plans targeted at protecting various seral stages of mixedwood habitat in addition to old aspen. However, the extent and configuration of such future old forest cover on the landscape sufficient to accomplish sustainable forest management policies remains unknown (Cummings et al., 1994).

At the point-count and forest-stand level, we found few differences in the richness and abundance of most ground- and shrub-nesting species. However, at the landscape level, we found that ground-nesting species were more common in young and old stands than in mature stands. We suspect that the dense shrub layer in mature stands may have limited the number of suitable nesting or foraging sites required by ground-nesting species. Yet, the most abundant ground-nesting bird in our study area was the ovenbird, which was most abundant in mature forest, indicating that not all ground-nesting species respond to shrub density and shrub type in the same manner. Beaked hazelnut was the dominant shrub in our study area. Unlike many shrubs, beaked hazelnut has little foliage at ground level and often has a well developed litter layer beneath it, which may provide a sufficiently open forest floor for species like the ovenbird.

At local scales, we found little effect of forest age on the richness and abundance of shrub-nesting birds. Instead, we found that forest stands, regardless of age, with higher deciduous shrub cover were more likely to have higher densities of shrub-nesters. In particular, stands with high densities of beaked hazelnut provided important nesting habitat for species such as American redstart, rose-breasted grosbeak, chestnut-sided warbler, and Canada warbler. Similar associations between high deciduous shrub density and the relative abundance of American redstart and Canada warbler have been found in western Alberta (Schieck et al., 1995), but there, these vegetation attributes were more

likely to occur on old stands of greater than 120 years. In contrast, Westworth and Telfer (1993) found that deciduous shrub cover was highest in 14-year-old stands in eastern Alberta, and suggested that this resulted in higher densities of American redstart and rose-breasted grosbeak.

Vegetation structure in similar-aged aspen forests in western Canada varies among regions. For example, Schieck et al. (1995) and Westworth and Telfer (1993) found mature forests in Alberta tend to be structurally less diverse than young or old forests due to low shrub density. Schieck et al. (1995) argued that this difference in structural heterogeneity among age-classes was linked to the tightly closed canopy in mature aspen that reduced light transmission to the forest floor (Huenneke, 1983; Levey, 1988; Peterson and Peterson, 1992). In contrast, we found that shrub density was highest in mature stands. Differences in shrub density between different forest age-classes in aspen forests in Alberta and Saskatchewan could be caused by a variety of factors. Beaked hazelnut tends to be more common in the southern portion of the boreal forest (Johnson et al., 1995). The studies conducted in Alberta tended to be farther north than our study area, where green alder (*Alnus crispa*) is more prevalent (Westworth and Telfer, 1993). Further, green alder tends to grow in more open forests than hazelnut (Johnson et al., 1995). Old aspen forest (>120 years) with low canopy closure, such as those studied by Schieck et al. (1995), are rare in Saskatchewan as natural succession often converts aspen-dominated forests into mixedwood stands of white spruce and aspen (Kabzems et al., 1986; Kirk et al., 1996). White spruce was a substantial component of our old stands, and may have been sufficiently dense to limit light penetration, and thus limit the shrub layer in our older forests. Hobson and Schieck (1999) recently contrasted bird communities in three age-classes of post-fire and post-harvest sites in aspen-dominated mixedwood forest in central Alberta. These authors found that the greatest divergence in bird communities between these two forms of disturbance occurred immediately (i.e. within one year) following disturbance but largely converged after 28 years. Differences between disturbance types was due primarily to the large volume of standing dead timber following fire, an attribute that had largely disappeared by 14 years postdisturbance. Our young post-harvest sites

were approximately the same age as those 23–26-year-old post-fire sites used by Schieck et al. (1995). However, our young sites showed the lowest species richness. We suspect that such differences between our study and that of Schieck et al. (1995) were driven largely by the denser (beaked hazelnut) shrub component occurring on our mature stands. Clearly, when making management decisions, components other than forest age and tree composition are required, but forest inventory data at the landscape level rarely provide information on subcanopy or snag/residual tree attributes. Given the importance of the shrub layer to many nesting birds and the way in which this component of stand structure varies with region, disturbance origin (i.e., fire versus harvest), and age, a more complete inventory of subcanopy structure is likely required on forest management areas (e.g., Finch and Reynold, 1988). Also, silvicultural techniques that ultimately create more optimal conditions for shrub-nesting species in young and mature stands (e.g. Easton and Martin, 1998) might allow more effective management of these species.

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References

Blondel, J., Ferry, C., Frochot, B., 1970. La methode des indices ponctuels d'abundance (ipa) ou des releves d'avifaune par "stations d'ecoute". Alauda 38, 55–71.

Bouman, O.T., Langen, G., Bouman, C.E., 1996. Sustainable use of the boreal Prince Albert Model Forest in Saskatchewan. For. Chron. 72, 63–72.

Collins, S.L., James, F.C., Risser, P.G., 1982. Habitat relationships of wood warblers (Parulidae) in north central Minnesota. Oikos 39, 50–58.

Colwell, R.L., 1987. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's guide and application published at: http://viceroy.eeb.uconn.edu/ estimates.

Cummings, S.G., Burton, P.J., Prahacs, S., Garland, M.R., 1994. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: a simulation study. For. Ecol. Manage. 68, 281–302.

Easton, W., Martin, K., 1998. The effect of vegetation management on breeding bird communities in British Columbia. Ecol. Applic. 8, 1092–1103.

Erskine, A.J., 1977. Birds in boreal Canada: communities, densities, and adaptations. Canadian Wildlife Service Report Series # 41. Ottawa, Ont., Canada

Finch, D.M., Reynold, A., 1988. Bird response to understory variation and conifer succession in aspen forests. In: Emerick, J., Foster, S., Hayden-Wing, L., Hodgson, J., Monarch, J., Smith, A., Thorne, O., Todd, J. (Eds.), Issues and Technology in The Management of Wildlife. Thorne Ecological Institute Boulder, CO, pp. 87–96.

Flack, J.A.D., 1976. Bird populations of aspen forests in western North America. American Ornithological Union Monographs. Tampa, FL, USA

Francis, J., Lumbis, K., 1979. Habitat relationships and management of terrestrial birds in northeastern Alberta. Alberta Department of the Environment and Environment Canada. Edmonton, Alberta. AOSERP Rep. 78.

Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59, 871–883.

Halvorsen, O.R., 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? J. Veget. Sci. 7, 289–292.

Hobson, K.A., Schieck, J., 1999. Changes in bird communities with boreal mixedwood forest during the first thirty years: contrasting the effects of harvest and wildfire. Ecol. Applic. 9, 849–863.

Huenneke, L.F., 1983. Understory response of canopy gaps caused by the death of Ulmus americana in central New York. J. Torrie Bot. Club 110, 170–175.

Hunter, Jr., M.L., 1990. Wildfire, forests, and forestry. Principles of Managing Forests for Biological Diversity. Prentice Hall, Englewood Cliffs, NJ, USA

James, F.C., Shugart, H.H., 1970. A quantitative method of habitat description. Audubon Field Notes 24, 727–735.

James, F.C., Rathbun, S., 1981. Rarefaction, relative abundance, and diversity of avian communities, and diversity of avian communities. Auk 98, 785–800.

James, F.C., Wamer, N.O., 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63, 159–171.

James, F.C., Hess, C.A., Kufrin, D., 1997. Species-centered environmental analysis: indirect effects of fire history on Red-Cockaded woodpeckers. Ecol. Applic. 7, 118–129.

Johnson, D., Kershaw, L., MacKinnon, A., Pojar, J., 1995. Plants of the western boreal and aspen parkland. Lone Pine Publishing, Edmonton, AB, Canada.

Kabzems, A., Kosowan, A.L., Harris, W.C., 1986. Mixedwood section in an ecological perspective. Technical Bulletin 8. Saskatchewan Parks and Renewable Resources. Regina, Saskatchewan.

Kirk, D.A., Diamond, A.W., Hobson, K.A., Smith, A.R., 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Can. J. Zool. 74, 1749–1770.

Land, D., Marion, W.R., O'Meara, T.E., 1989. Snag availability and cavity nesting birds in slash pine plantations. J. Wildl. Manage. 53, 1165–1171.

Lee, P.C., Crites, S., Nietfeld, M., Van-Nguyen, H., Stelfox, J.B., 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. 7, 691–701.

Levey, D.J., 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69, 1076–1089.

Lundquist, R.W., Mariani, J.M., 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range (USA). US Forest Service General Technical Report Pnw 0(285), 221-240.

McCune, B., Mefford, M.J., 1997. Multivariate analysis of ecological data, Version 3. MJM Software, Gleneden Beach, Oregon, USA

Moskat, C., Szekely, A., 1989. Habitat distribution of breeding birds in relation to forest succession. Folia Zoologica. 38, 363–376.

Peterson, E.B., Peterson, N.M., 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Canadian Forest Service – Canadian Northern Forestry Centre Special Report 1.

Ralph, C.J., Guepel, G.R., Master, T.R., Desante, D.F., 1992. Field methods for monitoring landbirds. USDA Forest Service. Redwood Sciences Laboratory, Arcata, California.

Schieck, J., Nietfeld, M., Stelfox, J.B., 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. Can. J. Zool. 73, 1417–1431.

Schmiegelow, F.K.A., Hannon, S.J., 1993. Adaptive management, adaptive science and the effects of forest fragmentation on boreal birds in northern Alberta. Trans. North Am. Wildl. Natural Res. Conf. 58, 584–598.

Schmiegelow, F.K.A., Machtans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78, 1914–1932.

Stelfox, J.B. (Ed.). 1995. Relationships between stand age stand structure and biodiversity in the aspen mixedwood forests in Alberta. Alberta Environmental Centre. Vegreville Alberta.

ter Braak, C.J., 1992. CANOCO – a Fortran program for canonical community ordination. Microcomputer Power, Ithaca, New York.

Thingstad, P.G., 1997. Challenges to conservation of biological diversity in boreal forestry landscape; a case study using bird guilds as environmental indicators. Fauna Norvegica Series C Cinclus 20, 49–68.

Van Wagner, C.E., 1968. The line intersect method for forest fuel sampling. For. Sci. 14, 20–26.

Walters, C.J., 1986. Adaptive Management of Natural Resources. McGraw-Hill, New York.

Welsh, C.J.E., Capen, D.E., 1992. Availability of nesting sites as a limit to woodpecker populations. For. Ecol. Manage. 48, 31–41.

Welsh, D.A., 1987. The influence of forest harvesting on mixed deciduous-coniferous boreal bird communities in Ontario, Canada. Acta Oecol. 8, 247–252.

Welsh, D.A., Lougheed, S.C., 1996. Relationships of bird community structure and species distributions to two environmental gradients in the northern boreal forest. Ecography 19, 194–208.

Westworth, D.A., Telfer, E.S., 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Can. J. For. Res. 23, 1830–1836.

Weyerhaeuser Canada., 1998. Twenty-year forest management plan & environmental impact statement. Weyerhaeuser Canada and Saskatchewan Environment and Resource Management. Prince Albert, Saskatchewan.

Willson, M.F., 1974. Avian community organization and habitat structure. Ecology 55, 1017–1029.

Willson, M.F., Comet, T.A., 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. Condor 98, 350–362.