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BIRD COMMUNITIES AND FOREST SUCCESSION IN THE SUBALPINE ZONE OF KOOTENAY NATIONAL PARK, BRITISH COLUMBIA

by

Daniel J. Catt

Dipl. T., British Columbia Institute of Technology, 1983
B. Sc. (Biol.), Simon Fraser University, 1987

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
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in the Department
of
Biological Sciences

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BIRD COMMUNITIES AND FOREST SUCCESSION IN THE SUBALPINE

ZONE OF KOOTENAY NATIONAL PARK, BRITISH COLUMBIA

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ABSTRACT

I examined successional stage, forest structure and forest edges as factors which contribute to the diversity of birds in subalpine forests of Kootenay National Park, British Columbia. In 1989 and 1990, a total of 75 circular breeding bird plots were censused in herb-shrub, pole-sapling, young, mature and old growth successional stages (3, 21, 65, 163 and 241 years post-fire respectively). Density, species richness and diversity of birds generally increased with stand age, although minor decreases occurred in young and old growth stages.

Increases in density and diversity are related to the development of diverse vegetation structure which increases with successional age of the forest. Structural components of the vegetation (canopy height, percent cover of different vegetation layers, foliage volume and densities of snags and stumps) are related to bird community characteristics as well as the occurrence of feeding and nesting guilds of birds.

To examine edge effects, transects were conducted across edges between the pole-sapling and old growth stages as well as between mature and old growth stages. Although bird densities were greater at edges than within the homogeneous interior of successional stages, they did not decrease with increasing distance from edge. Fires affect forest landscapes by creating a stand mosaic which increases habitat diversity of the forest. My results reveal that changes in subalpine bird communities follow these habitat alterations.

QUOTATION

" When the bird and the book disagree, always believe the bird."

- BIRDWATCHER'S PROVERB

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CHAPTER 1

GENERAL INTRODUCTION

Kootenay National Park, British Columbia, is one of the most diverse parks in western Canada. Its habitats range from glacier scoured alpine tundra to semi-desert grasslands. As a consequence, Kootenay National Park may be the only park in North America that contains both cacti and glaciers within its boundaries. Associated with these numerous habitats is a diverse fauna. Four amphibian, 3 reptile, 57 mammal and 193 bird species have been recorded in Kootenay National Park (Poll et al. 1984, personal observation).

Since 1979, Canadian Parks Service policy has suggested that natural processes, such as forest fires, should be allowed to fulfill their ecological role in national parks with the objectives of 1) perpetuating naturally occurring plant and animal species, 2) perpetuating naturally occurring vegetation patterns and mosaics, and 3) maintaining a natural fire regime. Wildfire is considered an important natural process in national park ecosystems (VanWagner and Methven 1980). Recent changes in policy reflect this position and the Canadian Parks Service is moving towards implementing vegetation and fire management programs. In Kootenay National Park, a fire management plan is being developed. One weakness of the plan is the lack of quantitative relationships between fire and wildlife (Alan Masters, personal communication). Wildlife species are individually adapted to combinations of plant community and successional stage for feeding or reproduction or both (Meslow and Wight 1975). Birds are useful indicators of habitat conditions because each species has its own distinctive breeding range and habitat requirements (Robbins 1979). Successful management of bird species depends on how well we understand their habitat requirements. Our ability to describe faunal communities and the consequences of habitat changes is vital to understanding the ecology of forest birds (Anderson 1972). The purpose of my study was to examine relationships between bird communities and forest succession in the subalpine zone of Kootenay National Park.

The three major characteristics of a bird community are its bird density, species richness and species diversity. Diversity may be measured most directly as number of species but in most wildlife community studies it is expressed as an index to both the variety and abundance of species. Two components of diversity are generally recognized: 1) richness, or the number of distinct taxa present and 2) evenness, the distribution of individuals among those taxa. Community diversity can be examined by noting the number of species within a single habitat (alpha-diversity), the changes in species composition along a series of habitats (beta-diversity), or the total species richness of a large geographic region (gamma-diversity) (Whittaker 1960). The number of species, density and diversity of breeding birds in a community are closely related to successional stage of the vegetation (Haapanen 1965, Meslow and Wight 1975), structure of the habitat (MacArthur and MacArthur 1961), and amount of edge or ecotone (Thomas et al. 1978).

Many researchers have examined bird community-vegetation interactions which occur during forest succession (Johnston and Odum 1956, Haapanen 1965, Karr 1968, Anderson 1972, Shugart and James 1973, Meslow and Wight 1975, Schwab 1979, Smith and MacMahon 1981, Helle 1985, Morgan and Freedman 1986, Moskat and Szekely 1989). Most studies have been conducted at low elevations in eastern deciduous or interior coniferous forests. Quantitative studies of bird communities within successional stages in subalpine forests have recently been conducted in the American Rocky Mountains (Taylor and Barmore 1980, Smith and MacMahon 1981, Finch and Reynolds 1987, Keller 1987, Scott and Crouch 1988) but not in the Canadian Rocky Mountains which can have different successional dynamics (Day 1972). In Chapter 2, I examine patterns of bird diversity, density and species richness along a subalpine sere in the southern Canadian Rocky Mountains. I also determine if each successional stage supports a unique complement of bird species.

Many researchers investigating bird community-vegetation interactions during the course of forest succession have found a general trend of increased bird diversity and abundance with successional age of the forest (Johnston and Odum 1956, Haapanen 1965, Anderson 1972, Shugart and James 1973, Meslow and Wight 1975, Shugart et al. 1978, Helle 1985). Shugart et al. (1978) suggest that this increase is associated with development of diverse vegetation structure which can be broadly equated to forest succession. As succession progresses, biomass increases and vegetation structure becomes more complex. These changes create more available niches and result in increased bird species diversity (Meslow 1978).

Structural components of the vegetation can sometimes be used to predict bird community characteristics such as abundance, species richness and species diversity (Balda 1975). In addition to having utility in predicting broad bird community characteristics, vegetation structure corresponds with the occurrence of particular bird species as well as guilds of species. In Chapter 3, I examine relationships between bird community characteristics and structural attributes of the vegetation. I also determine if nesting and feeding guilds of birds are related to vegetation structure.

Thomas et al. (1978) defined an "edge" as the area where two or more plant communities, or successional stages within plant communities, meet and an "ecotone" as the area influenced by the transition between these communities or successional stages. Edges and their associated ecotones are usually assumed to contain both more species and individuals than do homogeneous habitats on either side due to the intermixing of plant communities (Odum 1971). The resulting increased structural complexity provides life requisites that support greater numbers of species than do either habitat adjacent to the ecotone (Thomas et al. 1979a). The tendency for increased diversity and abundance at these plant community junctions is called "edge effect" (Odum 1971).

Only a few studies have quantified the "edge effect" in regards to density and diversity of nongame birds (Strelke and

Dickson 1980, Kroodsma 1982, Kroodsma 1984, Hansson 1983, Small and Hunter 1989). These studies have examined effects of abrupt induced edges created by clearcuts (Strelke and Dickson 1980, Hansson 1983) and powerlines (Kroodsma 1982, Kroodsma 1984, Small and Hunter 1989) as well as abrupt inherent edges along forest-river interfaces (Small and Hunter 1989). No studies have examined effects of fire induced edges or of edge contrast on bird communities. In Chapter 4, I determine if bird density, species richness and bird species diversity at the edge between two successional stages is greater than that found in homogeneous interior of each respective successional stage. I also determine if these differences in density, richness and diversity at the edge between two different successional stages decrease as contrast between the two successional stages decreases.

In Chapter 5, I discuss relationships between seral patterns of vegetation and bird communities in subalpine forests and examine their implications for fire management in Kootenay National Park.

STUDY AREA

The following description of Kootenay National Park is summarized from Volume II of the Park's Ecological Land Classification (Poll et al. 1984). Kootenay National Park occupies 1406 km^2 in the Rocky Mountains of southeastern B.C. (Fig. 1). In the park, there are four physiographic units that reflect geologic subdivision: the Main Ranges, with eastern and western sectors; the Western Ranges; and the Southern Rocky Mountain Trench.

Kootenay National Park has a continental macroclimate characterized by short, cool summers and long, cold winters. Owing to the predominant northwest-southeast orientation of the mountain ranges and valleys, which are nearly perpendicular to the prevailing westerly winds, there is a strong east-west gradient of temperature and precipitation. In addition to east-west variation in climate there are marked differences in climate between low and high elevations which are expressed as differences in vegetation physiognomy. Based on these climatic differences, Achuff et al. (1984) proposed an Ecological Land Classification and recognized three Ecoregions: Montane, Subalpine (with Lower and Upper portions) and Alpine (Fig. 2).

The Montane Ecoregion (< 1500 m) is limited to low elevations adjacent to the Columbia valley and along the Kootenay, lower Vermilion and Simpson Rivers. Climatically it is the warmest and driest ecoregion. The Montane Ecoregion has a drier climate than do ecoregions at higher elevations. Forests in this ecoregion are

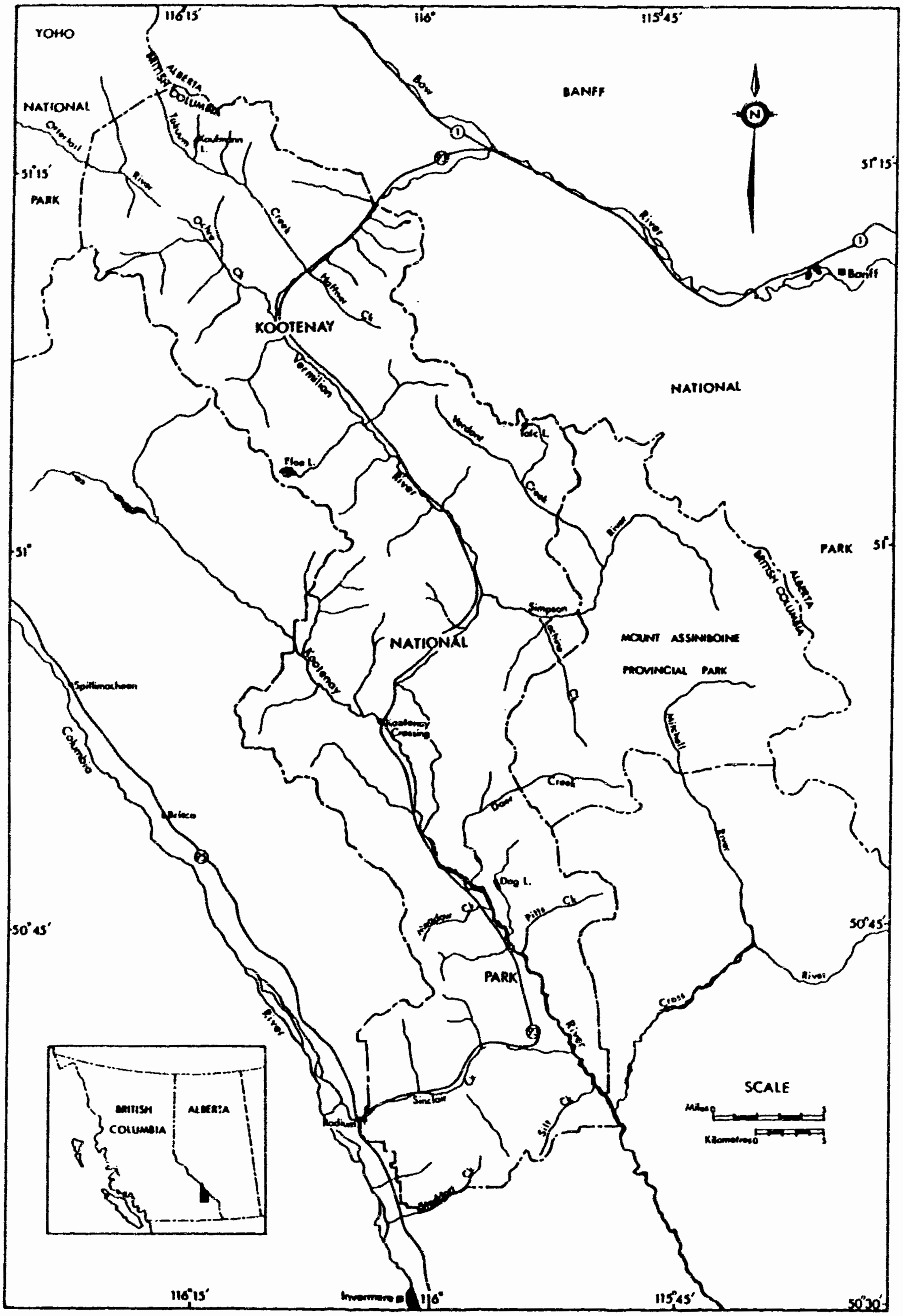

Figure 1. Location of Kootenay National Park, British Columbia and Banff National Park, Alberta (from Poll et al. 1984).

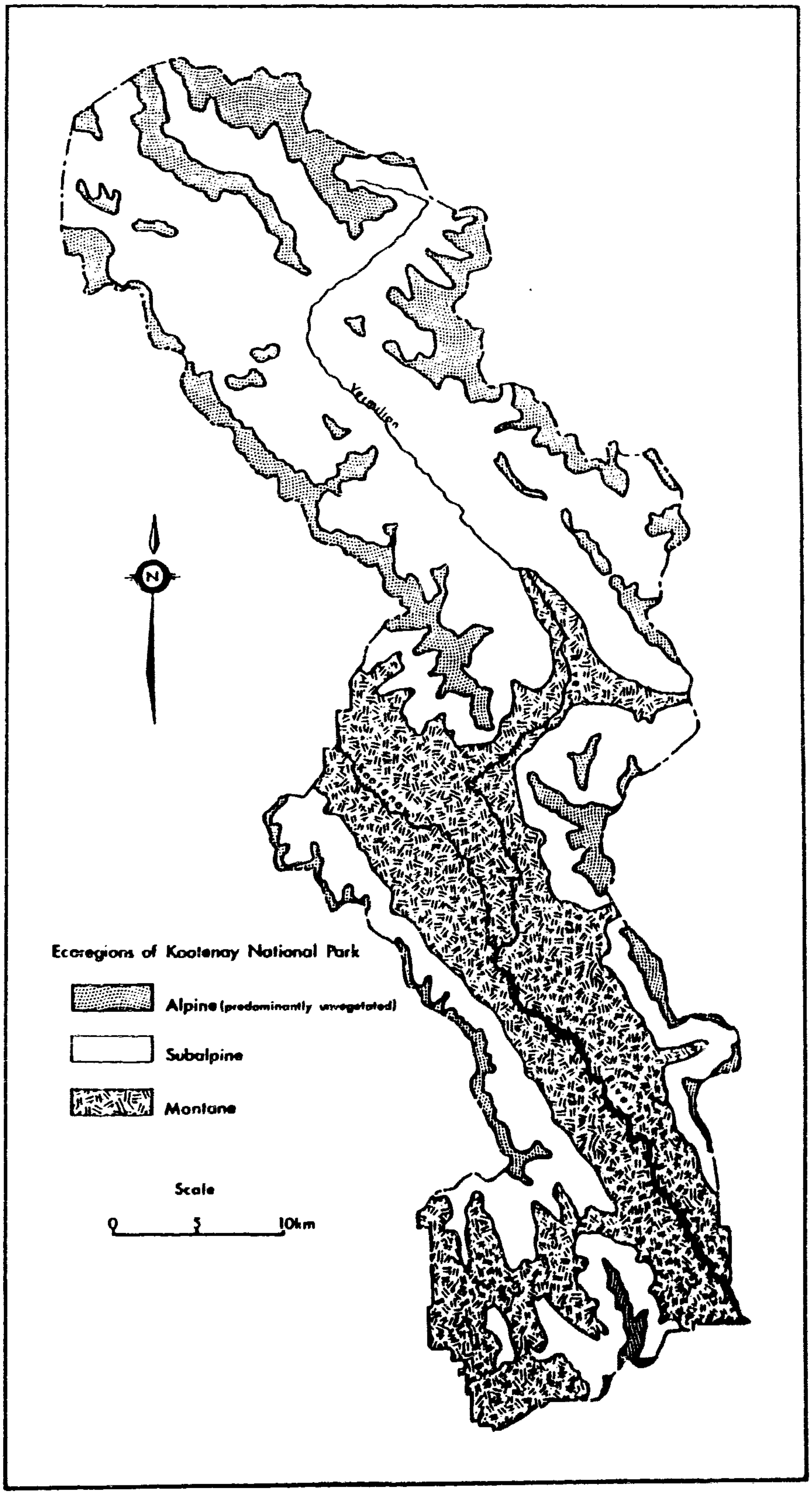

Figure 2. Ecoregions of Kootenay National Park, British Columbia (from Poll et al. 1984).

comprised of lodgepole pine *(Pinus contorta)*, Douglas fir *(Pseudotsuga menziesii)* and mixed forest. Dry grasslands occur but are restricted to the southwest portion of the park.

The Subalpine Ecoregion (1500 to 2300 m) is the most extensive ecoregion in Kootenay National Park. Precipitation is greater and temperatures cooler than in the Montane Ecoregion. The Lower Subalpine portion is characterized by extensive Engelmann spruce *(Picea engelmannii)*-subalpine fir *(Abies lasiocarpa)* closed canopy forests except where fires in the last 150 years have resulted in lodgepole pine forests. Climatically, the Lower Subalpine portion is milder and has less precipitation than does the Upper Subalpine portion. The Upper Subalpine portion is characterized by steep slopes with open canopy forests of Engelmann spruce-subalpine fir, subalpine larch *(Larix lyalli)*-subalpine fir or of mixed conifers. Shrubs and herb meadows occur on avalanche chutes. Treeline is the upper limit of this portion of the Subalpine Ecoregion.

The Alpine Ecoregion (> 2300 m) is higher, colder and receives more precipitation than do other ecoregions in the park. Tree growth is prevented by long, cold winters, short, cool summers and strong winds. Vegetation in this ecoregion is characterized by grasses, herbs and low shrubs.

My study was conducted in the Lower Subalpine portion of the Subalpine Ecoregion at elevations between 1500 and 1700 m. Achuff et al. (1984) and Poll et al. (1984) provide a detailed description of Kootenay National Park.

Successional Dynamics

The major tree species in the Lower Subalpine portion of the Subalpine Ecoregion include Engelmann spruce, subalpine fir and lodgepole pine. During wet years in the Rocky Mountains, frequent summer showers reduce the likelihood of lightning fires. However during dry years, fires are the predominant disturbance initiating secondary succession in subalpine spruce-fir forests (Day 1972). Based on a structural analysis of subalpine forests in southern Alberta, Day (1972) hypothesized a four phase post-fire successional sequence for a typical stand.

In the first phase (< 55 years post-fire) lodgepole pine is the most prevalent successional tree species, dominating large tracts of subalpine forest. Engelmann spruce establishes along with or shortly after lodgepole pine on the burned site. The dense canopy that is formed prevents further lodgepole pine reproduction while subalpine fir becomes established in the understory. In the second phase (55 to 150 years post-fire) Engelmann spruce begins to dominate the canopy, lodgepole pine declines and subalpine fir develops an all-aged understory. In the third phase (150 to 255 years post-fire), lodgepole pine becomes decadent or dies, Engelmann spruce dominates the canopy and subalpine fir dominates the understory. In the absence of disturbance (i.e. fire), a fourth and final phase (255 to 355 years post-fire) develops in which lodgepole pine is completely eliminated from the stand and the longer lived Engelmann spruce is dominant with a subordinated canopy layer composed mainly of subalpine fir. Extensive and frequent fires in the past, mainly initiated by dry electrical storms, prevented long-term successional development and maintained most of the forest in early lodgepole pine dominated phases of succession. Introduction of effective fire control, both inside and outside of national parks, is now permitting succession of the forest toward later stages.

CHAPTER 2

BIRD COMMUNITIES ALONG A SUBALPINE SERE

Since 1979, Canadian Parks Service policy (Parks Canada 1979) has suggested that natural processes, such as forest fires, should be allowed to fulfil their ecological role in national parks with the objectives of 1) perpetuating naturally occurring plant and animal species 2) perpetuating naturally occurring vegetation patterns and mosaics and 3) maintaining a natural fire regime. Before implementing park specific fire management plans the Canadian Parks Service recognizes the need to understand how natural processes, such as fire, affect wildlife and their habitats. The purpose of my study was to examine relationships between bird communities and forest succession in the subalpine zone of Kootenay National Park, British Columbia.

Many researchers have examined bird community-vegetation interactions which occur during forest succession (Johnston and Odum 1956, Haapanen 1965, Karr 1968, Anderson 1972, Shugart and James 1973, Meslow and Wight 1975, Schwab 1979, Smith and MacMahon 1981, Helle 1985, Morgan and Freedman 1986, Moskat and Szekely 1989). While each study shows that many bird species are selective of successional stage, the studies differ regarding patterns of bird diversity and abundance during succession. The general pattern common to the majority of studies is that bird diversity and abundance increase with successional age. Although this broad pattern occurs, diversity and abundance may decrease slightly during mid-successional stages (Johnston and Odum 1956, Haapanen 1965, Shugart and James 1973, Meslow and Wight 1975, Schwab 1979, Helle 1985) or during the climax stage (Karr 1968, Anderson 1972, Smith and MacMahon 1981). Most studies have been conducted in low elevation coniferous or eastern deciduous forests. Quantitative studies of bird communities among successional stages in subalpine forests have been conducted in the American Rocky Mountains (Taylor and Barmore 1980, Smith and MacMahon 1981, Finch and Reynolds 1987, Keller 1987, Scott and Crouch 1988) but not in the Canadian Rocky Mountains, which can have different successional dynamics (Day 1972). My objectives were 1) to examine patterns of bird diversity, density and species richness along a subalpine sere in the southern Canadian Rocky Mountains and 2) to determine if each successional stage supported a unique complement of bird species.

METHODS

Choice of Plots in Successional Stages

Before going into the field, potential census areas at which to sample successional stages in the Lower Subalpine portion of the Subalpine Ecoregion were located on a 1:50,000 fire history map of Kootenay National Park (Masters 1989). These areas were then viewed in the field. Three of the census areas chosen were within Kootenay National Park, one was located on the Banff National Park side of the Continental Divide and the last was located just outside the western boundary of Kootenay National

Park. Five successional stages were identified: 1) herb-shrub, 2) pole-sapling, 3) young forest, 4) mature forest and 5) old growth forest (3, 21, 65, 163, and 241 years post-fire respectively) (Table 1). Because there have not been any recent large fires in the Lower Subalpine of Kootenay National Park, clearcut patches outside the park boundary were used to represent an herb-shrub successional stage. The pole-sapling stand originated as a result of a forest fire in 1968 and is almost exclusively pole sized lodgepole pine. Because no homogeneous stands of lodgepole pine in young successional stages (approximately 65 years old) occur in the Lower Subalpine of Kootenay National Park a site in Banff National Park was used. The mature successional stage is common in the Lower Subalpine of Kootenay National Park and is comprised of mixed lodgepole pine, Engelmann spruce, and subalpine fir approximately 150 years of age. The old growth stage originated from wildfire in the mid 1700's and is comprised almost exclusively of Engelmann spruce and subalpine fir. All five successional stages that I censused are in the Lower Subalpine at elevations between 1500 and 1700 m.

Bird Censuses

Birds were inventoried using the variable circular plot method (Reynolds et al. 1980) where the observer remains stationary and estimates the horizontal distance to each bird observed. This method was designed for structurally complex vegetation types and rugged terrain and because it accounts for

Table 1. Mean values of vegetation measurements (± SE) in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks.

	Successional Stage				
	Herb-shrub	Pole-sapling	Young	Mature	Old growth
Number of plots	40	72	60	64	68
Canopy height[a]	0.7 ± 0.0	4.1 ± 0.1	13.7 ± 0.2	22.1 ± 0.4	23.2 ± 0.2
Herb cover[b]	30.0 ± 3.2	77.9 ± 2.3	43.2 ± 2.8	55.4 ± 2.7	52.6 ± 2.2
Low shrub cover[c]	11.9 ± 1.9	37.3 ± 2.1	31.3 ± 2.2	26.5 ± 2.0	36.7 ± 1.9
High shrub cover[d]	2.2 ± 0.9	23.3 ± 1.8	17.1 ± 1.8	30.9 ± 2.7	46.2 ± 2.7
Main canopy cover[e]	0.0	0.0	39.9 ± 3.2	29.5 ± 2.1	28.5 ± 2.2
High canopy cover[f]	0.0	0.0	0.7 ± 0.5	15.1 ± 2.2	17.6 ± 2.6
Total cover[g]	44.1	138.5	132.2	157.4	181.6

[a] Canopy height = height of dominant trees or bushes (m)

[b] Herb cover = total percent foliage cover in the 0.0 - 0.5 m layer

[c] Low shrub cover = total percent foliage cover in the 0.5 - 1.0 m layer

[d] High shrub cover = total percent foliage cover in the 1.0 - 10.0 m layer

[e] Main canopy cover = total percent canopy closure in the 10.0 - 20.0 m layer

[f] High canopy cover = total percent canopy closure > 20.0 m

[g] Total cover = b+c+d+e+f (maximum possible = 500 percent)

differing bird detectabilities between vegetation types, absolute densities can be determined (although the reliability of the density values is dependent on the observers proficiency at distance estimation). Within each successional stage, transects were located on aerial photographs and then established on the ground. From about 0.5 hours before sunrise until 10:00 am MDT, plots were sampled along the transects at sites 200 m apart. In 1989, 9 plots were established in the herb-shrub stage and 10 plots in each of the other stages. In 1990, 5 of the 10 plots sampled during 1989 in the pole-sapling, young, mature and the old growth stages were resurveyed. In addition to these plots, 8, 5, 6 and 7 new plots were surveyed in the pole-sapling, young, mature and old growth stages respectively. During 1989 and 1990 combined, 75 different circular plots were established. At the centre of each plot I remained stationary for one minute before beginning to record bird activity for a 10 minute period. Each bird seen or heard was identified to species and recorded on a field sheet. The circular plot was divided into 10 m intervals of radius out to 100 m and the distance to each bird, at the location it was first seen or heard, was estimated and plotted on a field sheet. I also recorded species detected between 100 m and 250 m. Each record was noted as being visual, song, call, or an overflight. Most plots were censused 4 times within a field season. All censuses were conducted between 1 June and 30 June in both years. I conducted all censuses to eliminate inter-observer bias.

Calculation of Bird Densities

Because of differences in vegetation structure among successional stages an effective detection distance should be determined for each species in each successional stage. I determined effective detection distances for all bird species detected a minimum of 20 times within a successional stage over the entire sampling period. Of the 28 detection distances calculated, 25 (89 %) were 90 m or greater. Only 4 species were abundant enough to calculate detection distances across three or more successional stages. Of these 4 species, 3 had equal detection distances in all stages while the fourth had 3 detection distance radii of 100 m and 1 of 90 m. I concluded that under these conditions use of the 100 m detection distance radius for all species, rather than adjusted radii, was suitable for estimating densities (see also Finch and Reynolds 1987, Raphael 1987, and Moskat and Szekely 1989). Following Franzreb (1976), when calculating densities, I used either the sum of all songs, calls and visual sightings of a species or the number of songs times 2 (to account for the mate of the territorial male), whichever was greater.

Treatment of Bird Data

For each 100 m radius plot, I totalled the number of individuals as well as the number of species detected (species richness, S). Bird species diversity/plot (H) was then calculated. To facilitate comparison of my results with other studies, I used the average of the four counts at each plot for my estimates of bird density, species richness and diversity. Use of the mean rather than the maximum of the four counts likely results in slightly lower estimates of these bird community indices. Bird species diversity was calculated using the Shannon-Weaver (Shannon and Weaver 1949) diversity index:

$$H = - \Sigma\, p_i \log_e p_i$$

where p_i is the proportion of species i of the total number of individuals in the plot. Bird species equitability (J) was calculated using:

$$J = H/\log_e S$$

where S is species richness. Habitat amplitude (HA) of each species was calculated using Simpson's index (Simpson 1949):

$$HA = 1 \Big/ \sum_{h=1}^{n} p_i^2$$

where p_i is the proportion of density of species i in successional stage h in relation to the sum of its densities in all of the n successional stages. Percent similarity of bird communities between successional stages was calculated using Renkonen's index (Renkonen 1938):

$$\text{Percent Similarity} = \Sigma \min (p_{i1}, p_{i2})$$

where p_{i1} and p_{i2} are the proportions (in percent) of the ith species in successional stages 1 and 2 respectively. Densities of flocking species such as Pine Siskins and White-winged Crossbills were not calculated and were not used in the calculation of diversity.

Vegetation Analysis

Four vegetation plots, 4.5 m in radius, were sampled at 50 m intervals across the diameter of each circular bird plot. For each vegetation plot, percent cover was estimated for five vegetation layers: 0.0-0.5 m, >0.5-1.0 m, >1.0-10.0 m, >10.0-20.0 m, and >20.0 m. Percent canopy closure was visually estimated, and mean crown depth was measured, for each tree species present. Using crown depth and percent canopy closure, crown volume was calculated for each tree species. Foliage height diversity was calculated using the Shannon-Weaver index; where p_i = percent herb cover, percent low shrub cover, percent high shrub cover, percent main canopy closure or percent high canopy closure. Total cover was the sum of percent covers of all five vegetation layers (maximum possible: 500 %) and is intended to be a broad measure of cover and volume of vegetation (Karr and Roth 1971, Willson 1974).

RESULTS

General Patterns of the Bird Community

Bird species encountered during bird censuses in each successional stage are listed in Table 2. For each year, mean bird density (Fig. 3) and mean species richness/plot (Fig. 4) were calculated for the different successional stages. Bird densities differed significantly (Anova, $P < 0.05$) among successional stages

Table 2. Mean densities (individuals/40 ha) of birds encountered in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, during the breeding season, 1989-90. Standard errors are indicated in brackets below the densities.

	Successional stage								
	Herb-shrub	Pole-sapling		Young		Mature		Old growth	
Species	1989[a]	1989	1990	1989	1990	1989	1990	1989	1990
Spruce Grouse	-[b]	3.0 (1.3)	3.8 (1.2)	3.8 (1.7)	6.4 (2.0)	7.0 (1.9)	3.5 (1.2)	6.9 (1.9)	1.6 (0.9)
Northern Hawk-Owl	-	+[c]	-	-	-	-	-	-	-
Black Swift	-	-	-	-	-	-	-	F[d]	F
Rufous Hummingbird	-	-	0.5 (0.5)	-	-	-	-	0.4 (0.4)	-
Hairy Woodpecker	-	-	-	-	-	-	-	-	0.3 (0.3)
Three-toed Woodpecker	-	-	-	-	-	2.9 (1.5)	-	1.5 (1.0)	-
Northern Flicker	-	1.7 (1.0)	2.8 (1.1)	0.6 (0.6)	1.3 (0.9)	0.6 (0.6)	1.6 (0.9)	1.5 (1.0)	1.1 (0.7)
Pileated Woodpecker	-	-	+	-	-	-	-	-	-
Olive-sided Flycatcher	-	2.0 (1.1)	2.6 (1.0)	-	-	-	0.5 (0.5)	4.4 (1.6)	0.8 (0.6)
Western Wood Pewee	-	-	-	-	0.3 (0.3)	-	0.3 (0.3)	-	-
Hammond's Flycatcher	-	-	-	-	-	0.3 (0.3)	-	-	-
Dusky Flycatcher	-	3.4 (1.4)	9.9 (1.7)	-	-	-	-	-	-
Gray Jay	-	-	-	-	5.7 (1.7)	0.3 (0.3)	2.7 (1.1)	0.7 (0.7)	2.9 (1.2)

Clark's Nutcracker	-	2.0 (1.1)	0.2 (0.2)	-	-	-	0.3 (0.3)	0.7 (0.5)	-
Common Raven	F	F	F	F	F	-	-	-	-
Black-capped Chickadee	-	-	-	-	-	-	-	3.6 (1.9)	-
Mountain Chickadee	-	1.3 (0.9)	-	1.9 (1.1)	-	6.7 (2.4)	0.3 (0.3)	0.7 (0.7)	-
Boreal Chickadee	-	-	-	4.8 (1.8)	3.5 (2.1)	2.6 (1.5)	3.7 (1.7)	0.7 (0.7)	5.8 (2.2)
Red-breasted Nuthatch	-	0.7 (0.7)	1.2 (0.7)	-	-	2.9 (1.2)	12.5 (2.4)	2.9 (1.3)	12.7 (2.3)
Brown Creeper	-	-	-	0.6 (0.6)	-	-	2.1 (1.3)	-	1.6 (0.9)
Winter Wren	-	-	-	-	-	1.3 (0.9)	3.7 (1.3)	5.8 (2.1)	10.1 (2.0)
Golden-crowned Kinglet	-	-	-	3.2 (1.6)	6.7 (2.1)	18.1 (3.6)	20.4 (2.5)	11.6 (3.0)	27.1 (3.9)
Ruby-crowned Kinglet	-	-	-	4.5 (1.5)	17.2 (2.3)	0.6 (0.6)	2.7 (1.1)	0.7 (0.7)	-
Townsend's Solitaire	6.2 (1.7)	4.4 (1.5)	1.7 (0.8)	-	-	-	-	-	-
Swainson's Thrush	-	10.7 (2.3)	22.4 (2.8)	8.0 (2.3)	15.9 (2.7)	15.3 (3.2)	18.3 (2.8)	13.8 (3.2)	23.3 (3.6)
Hermit Thrush	-	12.1 (2.7)	7.1 (1.7)	1.0 (0.7)	-	2.6 (1.1)	0.8 (0.6)	1.5 (1.0)	2.1 (1.0)
American Robin	3.5 (1.5)	3.4 (1.3)	5.9 (1.4)	1.3 (0.9)	1.0 (0.7)	9.2 (2.2)	3.2 (1.5)	5.8 (2.0)	1.3 (0.7)
Varied Thrush	-	-	0.2 (0.2)	7.3 (2.2)	6.7 (1.8)	4.5 (1.9)	5.6 (1.7)	1.1 (0.8)	6.9 (1.8)
Bohemian Waxwing	-	2.0 (0.9)	0.7 (0.5)	1.3 (0.6)	0.6 (0.4)	1.3 (0.8)	1.3 (0.7)	0.7 (0.5)	2.7 (1.1)
Tennessee Warbler	-	-	-	-	-	1.3 (0.9)	-	-	-
Orange-crowned Warbler	-	-	-	-	-	-	-	0.7 (0.7)	-
Yellow-rumped Warbler	-	8.4 (2.3)	17.0 (2.4)	8.6 (2.1)	16.6 (2.5	15.3 (3.1)	15.1 (2.5)	4.7 (2.0)	8.5 (2.2)

Townsend's Warbler	-	-	-	25.5 (3.6)	15.9 (3.1)	76.4 (6.6)	87.3 (6.5)	61.1 (6.5)	80.6 (5.0)
MacGillivray's Warbler	-	-	0.9 (0.7)	-	-	3.8 (1.5)	1.1 (0.7)	-	-
Wilson's Warbler	-	15.4 (3.0)	22.6 (3.0)	5.1 (1.6)	3.2 (1.3)	-	0.5 (0.5)	9.3 (2.6)	5.8 (2.1)
Chipping Sparrow	0.8 (0.8)	-	3.8 (1.2)	-	-	0.6 (0.6)	1.6 (0.9)	2.9 (1.4)	3.7 (1.5)
Fox Sparrow	-	-	0.5 (0.5)	-	-	-	-	-	2.1 (1.0)
Lincoln's Sparrow	-	-	-	-	-	1.9 (1.1)	1.6 (0.9)	-	-
Dark-eyed Junco	41.3 (4.8)	21.4 (2.8)	21.7 (2.3)	3.2 (1.3)	4.8 (1.6)	20.4 (3.4)	12.2 (2.4)	18.9 (3.5)	11.7 (2.2)
White-winged Crossbill	-	-	-	-	-	P[e]	P	P	P
Pine Siskin	P	P	P	P	P	P	P	P	P
Evening Grosbeak	-	-	-	-	-	1.6 (0.7)	0.3 (0.3)	-	-
TOTAL DENSITY	51.8	91.9	125.5	80.7	105.8	197.5	203.2	162.6	212.7
TOTAL SPECIES RICHNESS	5	17	21	17	16	26	28	27	23
TOTAL SPECIES DIVERSITY	0.68	2.30	2.31	2.30	2.34	2.25	2.15	2.32	2.22
TOTAL SPECIES EQUITABILITY	0.49	0.85	0.78	0.83	0.86	0.71	0.66	0.72	0.76
NUMBER OF PLOTS	9	10	13	10	10	10	11	10	12
TOTAL AREA SURVEYED (ha)	28.3	31.4	40.8	31.4	31.4	31.4	34.6	31.4	37.7

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[a] herb-shrub stage was censused only in 1989
[b] "-" not present in stage
[c] "+" present in stage but not within plot boundaries
[d] "F" observed flying over but not interacting with vegetation
[e] "P" present but density not calculated

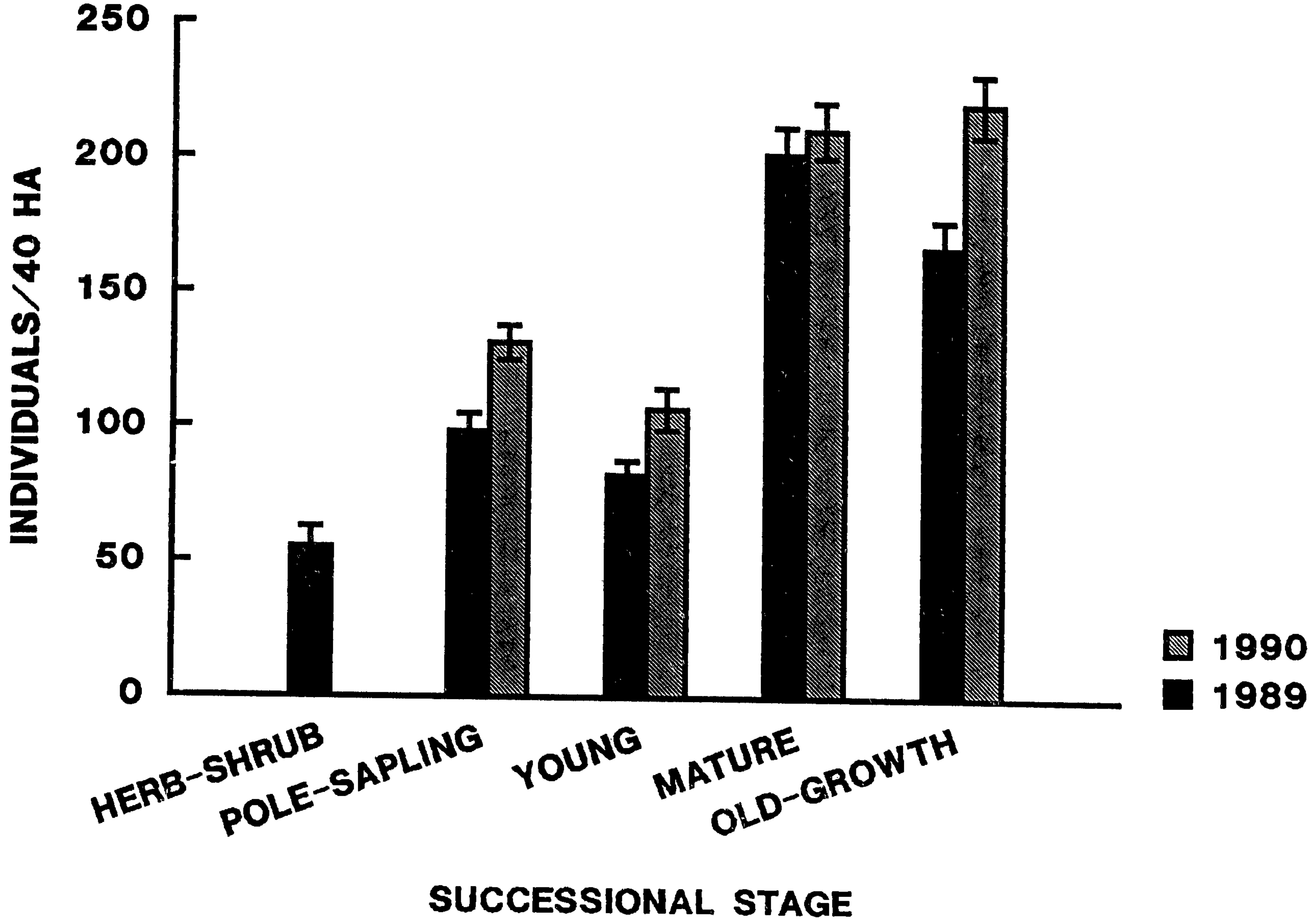

Figure 3. Mean densities of birds in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, during the breeding season, 1989-90 (standard errors are indicated).

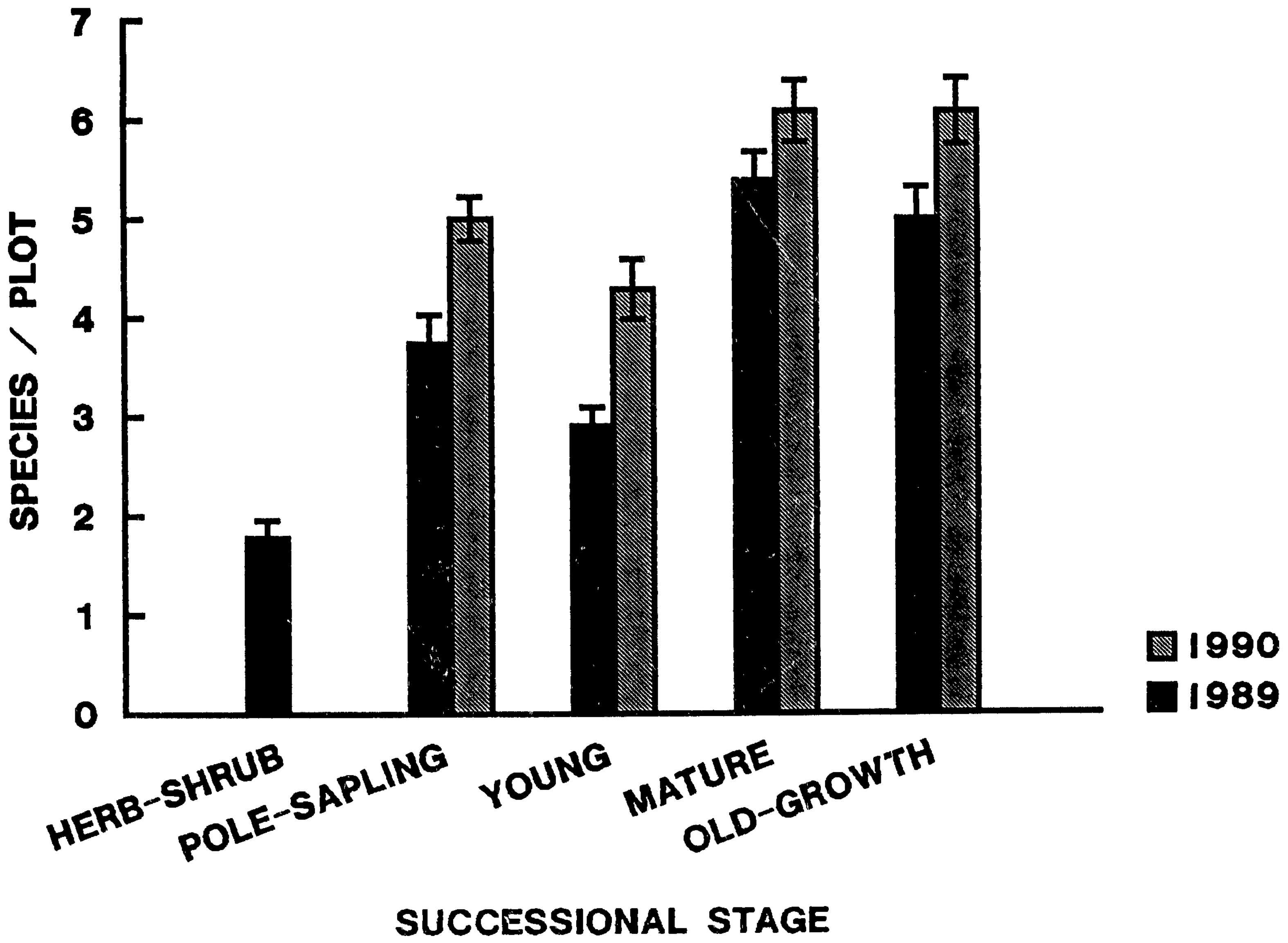

Figure 4. Mean species richness/plot (number of bird species/100 m radius plot) in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, during the breeding season, 1989-90 (standard errors are indicated).

in both 1989 and 1990. However differences between the pole-sapling and young stages in 1989 as well as between the mature and old growth stages in both years were not significant (Tukey test, $P > 0.05$). In 1989, bird density tended to increase with successional age but with modest decreases in density in the young and old growth stages. The same pattern was evident in 1990, but bird densities increased rather than decreased in the old growth stage. Bird density was greater (t-test, $P < 0.05$) in 1990 compared with 1989 in all successional stages censused, except the mature stage which did not differ between years (t-test, $P > 0.05$).

The patterns of species richness/plot for the two years are similar to those of bird density. Species richness/plot differed (Anova, $P < 0.05$) among successional stages in both years although differences between the pole-sapling and young stages and between the mature and old growth stages were not significant (Tukey test, $P > 0.05$). Furthermore, differences between pole-sapling and mature as well as pole-sapling and old growth stages were not significant (Tukey test, $P > 0.05$) in 1990. In 1989, there was a trend of increasing species richness/plot with decreases in the young and old growth stages. The same pattern was evident in 1990 but there was a slight increase rather than a decrease in species richness/plot in the old growth stage. Species richness/plot was greater in 1990 than in 1989 in all successional stages censused (t-test, $P < 0.05$), except the mature stage (t-test, $P > 0.05$).

Bird diversity/plot differed among successional stages

(Anova, $P < 0.05$) in 1989 but not in 1990 (Anova, $P > 0.05$). There were no differences in 1990, in part because the herb-shrub seral stage was not censused in 1990 (Fig. 5). In 1989, differences between pole-sapling and young, pole-sapling and mature, pole-sapling and old growth, and between mature and old growth stages were not significant (Tukey test, $P > 0.05$). In 1989, there was a pattern of increasing bird diversity/plot with successional age similar to the patterns of bird density (Fig. 3) and species richness/plot (Fig. 4). Bird diversity/plot was greater in 1990 compared with 1989 in the pole-sapling and young stages (t-test, $P < 0.05$) but not in the mature or old growth stages (t-test, $P > 0.05$). Because of this greater relative increase in the pole-sapling and young stages, compared to the mature and old growth stages, bird diversity/plot did not differ among successional stages in 1990.

Habitat Distribution of Species

There were differences in species distribution between early successional and late successional stages (Table 2). Townsend's Solitaire was encountered only in herb-shrub and pole-sapling stages. Dusky Flycatcher was exclusive to the pole-sapling stage. Northern Hawk-Owl and Pileated Woodpecker were also recorded only in the pole-sapling stage but due to the rarity of these species it is difficult to ascertain if they are exclusive to this stage. Gray Jay, Boreal Chickadee, Brown Creeper, Golden-crowned Kinglet, Ruby-crowned Kinglet, and Townsend's Warbler were found in all of

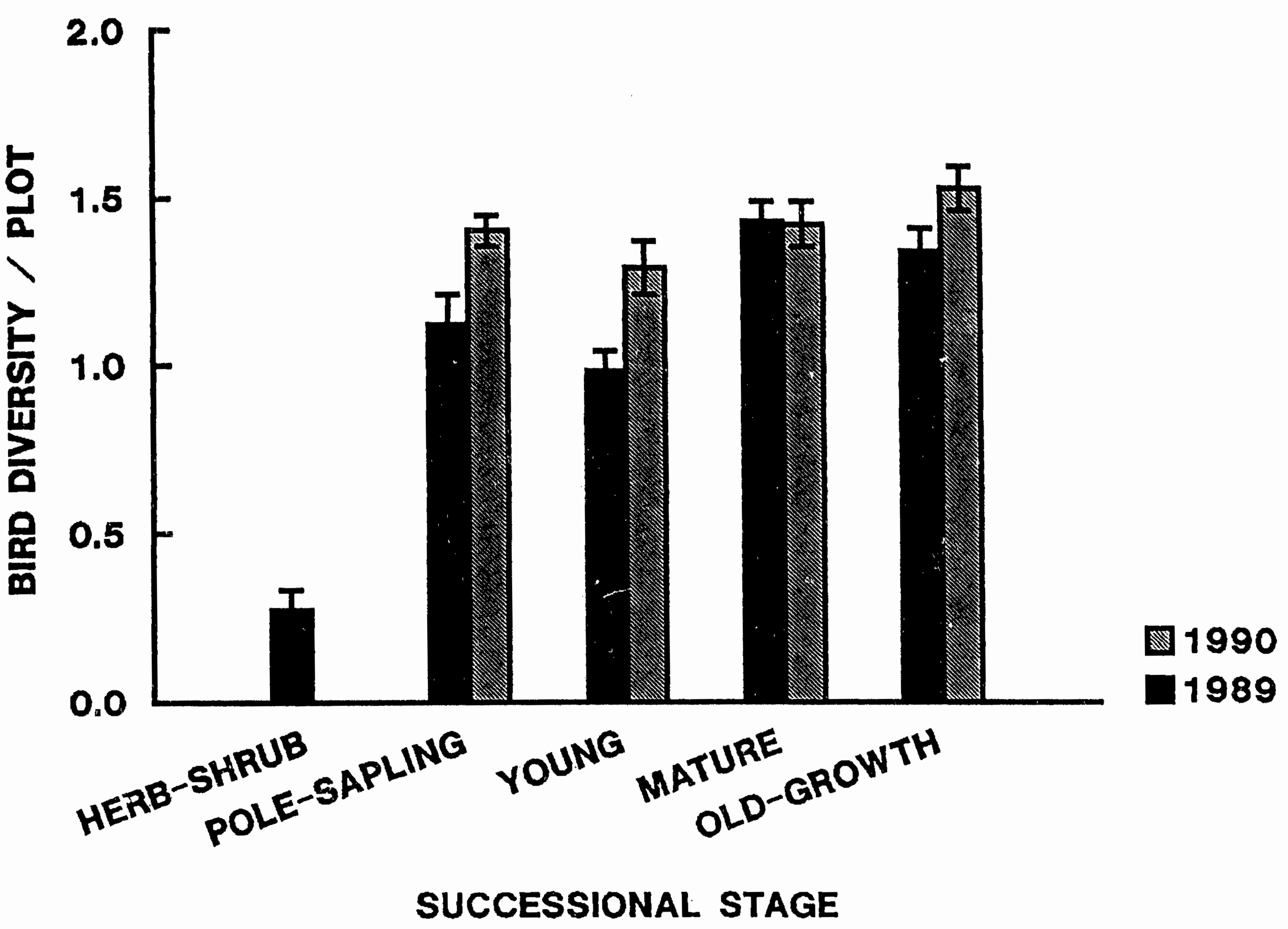

Figure 5. Mean bird diversity/plot (mean bird diversity/100 m radius plot) in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, during the breeding season 1989-90 (standard errors are indicated).

the three oldest successional stages (young, mature and old growth). Tennessee Warbler, Lincoln's Sparrow and Evening Grosbeak were recorded only in the mature stage while Hairy and Three-toed Woodpeckers, Black-capped Chickadee and Orange-crowned Warbler were encountered only in the old growth stage. Spruce Grouse, Northern Flicker, Red-breasted Nuthatch, Swainson's, Hermit and Varied Thrushes, Bohemian Waxwing as well as Yellow-rumped and Wilson's Warblers were found in all stages except herb-shrub. American Robin, Dark-eyed Junco and Pine Siskin were the only species found in all stages. There were no species exclusive to either the herb-shrub or young stages.

Habitat amplitudes and dominance values of most frequently observed species are shown in Table 3. Habitat generalists (eg. American Robin) have high habitat amplitude values while habitat specialists (eg. Dusky Flycatcher) have low habitat amplitude values. The dominance value indicates the rarity of a species (low for rare species, high for common species). There was no relationship between habitat amplitude and dominance.

Relationships Among Bird Communities

The similarities between consecutive stages increases from earliest to latest stages (Table 4). The herb-shrub stage was most similar to the pole-sapling stage, the pole-sapling to the young stage, the young to the mature stage and the mature to the old growth stage.

Table 3. Habitat amplitude and dominance of the more frequently observed bird species in the Lower Subalpine of Kootenay and Banff National Parks, during the breeding season, 1989-90. Species are arranged in order of decreasing habitat amplitude.

Species	Stages Present[a]	Habitat Amplitude	Dominance[b]
American Robin	1,2,3,4,5	4.19	2.8
Spruce Grouse	2,3,4,5	3.89	2.3
Swainson's Thrush	2,3,4,5	3.89	11.1
Bohemian Waxwing	2,3,4,5	3.79	1.4
Yellow-rumped Warbler	2,3,4,5	3.75	6.7
Dark-eyed Junco	1,2,3,4,5	3.58	10.9
Chipping Sparrow	1,2,4,5	3.10	0.9
Boreal Chickadee	3,4,5	2.97	1.4
Varied Thrush	2,3,4,5	2.94	2.3
Gray Jay	3,4,5	2.83	1.0
Golden-crowned Kinglet	3,4,5	2.47	6.2
Townsend's Warbler	3,4,5	2.47	23.5
Red breasted Nuthatch	2,3,4,5	2.34	2.5
Wilson's Warbler	2,3,4,5	2.33	5.0
Hermit Thrush	2,3,4,5	1.90	1.9
Townsend's Solitaire	1,2	1.75	0.9
Winter Wren	4,5	1.57	1.4
Dusky Flycatcher	2	1.00	1.0

[a] Stages are 1 = herb-shrub, 2 = pole-sapling, 3 = young, 4 = mature, 5 = old growth

[b] Dominance = $\dfrac{\text{total \# of registrations of species i}}{\text{total \# of registrations of all species}} \times 100$

Table 4. Renkonen's similarity index of bird community composition in the Lower Subalpine of Kootenay and Banff National Parks, during the breeding season, 1989-90.

	Successional Stage			
	Herb-shrub	Pole-sapling	Young	Mature
Pole-sapling	28[a]			
Young	5	42		
Mature	12	35	65	
Old growth	11	39	61	84

[a] a high index value indicates high similarity between two successional stages

DISCUSSION

In Kootenay National Park, patterns of bird density and species richness in relation to successional stage are similar to those observed elsewhere (Haapanen 1965, Shugart and James 1973, Melsow and Wight 1975, Schwab 1979, Helle 1985). I expected that the pattern of bird diversity in my study area would be similar to those of bird density and species richness. However, total bird diversity among successional stages (Table 2) and bird diversity/plot (Fig. 5) do not exhibit the same pattern as those for density and species richness. Although the trend of increasing bird diversity/plot with successional age evident in 1989 was not significant in 1990, this lack of significance was in part due to the herb-shrub stage not being censused in 1990. Interannual variability in density and diversity of birds is common in field studies (Anderson et. al. 1981, Helle and Monkkonen 1986, Szaro and Balda 1986, Keller 1987). When data for the two years are combined, bird diversity/plot increases with successional age (Anova, $P < 0.05$). Because of this interannual variation, it is reasonable to question the existence of a real pattern of increasing diversity with increasing successional age. Diversity indices such as those produced with the Shannon Weaver index, are affected by both number of species and evenness of species density among habitat types. Hence, most diversity indices are more sensitive to dominant species than they are to rare species. Because of this dependence on evenness, total bird diversity in the mature and old growth stages was similar to those in the pole-sapling and young stages despite mature and old growth stages having more species and almost twice the total density of birds as the pole-sapling and young stages (Table 2). This apparent similarity in total diversity is due to high densities of Townsend's Warbler in the two oldest successional stages (Table 4). By removing this species, diversity increases in the mature stage (2.58, 1989; 2.57, 1990), and in the old growth stage (2.66, 1989; 2.51, 1990).

General trends of increasing bird diversity and abundance with successional age evident in my study area are similar to those reported by a number of researchers (Johnston and Odum 1956, Karr 1968, Schwab 1979) but are opposite to those found by Taylor and Barmore (1980) who examined succession of birds in subalpine forests of Yellowstone and Grand Teton National Parks. Taylor and Barmore (1980) found a declining trend in both total density and total diversity from youngest to oldest successional stages. In their study, bird species diversity (measured using the Shannon-Weaver index) was greatest in moderately burned (40 % or more of the tree overstory was alive one year post-fire and part of grass-forb and low shrub layers were unburned) spruce-fir forests, one to three years post-fire. They attributed both increased density and diversity, in the first three years following fire, to a post-fire increase in the abundance of woodpeckers.

Although I used clearcuts outside Kootenay National Park as my early successional stage, I am not asserting that clearcutting is analogous to a catastrophic stand replacing fire. Two habitat elements that contribute to bird habitat value of older forests are standing, large, dead trees (snags and stumps) and fallen logs (Harris 1984). These structural features are also important to the habitat value of post-fire forests. The clearcuts that I surveyed are structurally similar to a post-fire subalpine forest only in the percent cover of the herb and shrub layers. Other important structural features such as dead and down woody material (Maser et al. 1979) and snags and stumps (Thomas et al. 1979b) were not represented on the clearcuts. These structural features are typical of a post-fire habitat so their absence may result in the absence of bird species which might otherwise be present. Examples of such birds include air sallying flycatchers, woodpeckers, primary cavity nesting birds and secondary cavity nesting birds including the Mountain Bluebird *(Sialia currucoides)*. Northern Three-toed Woodpeckers and Olive-sided Flycatchers were listed as common by Edwards (1972) four years post-fire in the Vermilion Pass burn area of Kootenay National Park.

The absence of Mountain Bluebirds in my censuses illustrates the dynamics of bird-successional stage relationships. Typically, Mountain Bluebirds are found in open habitats. They breed in recently burned habitats of Kootenay National Park (Munro and Cowan 1944, Edwards 1972, Scott 1973, O'Keefe 1975). Mountain bluebirds were observed in the Vermilion Pass burn four (Edwards 1972), five (Scott 1973) and seven years (O'Keefe 1975) post-fire and were the fifth most common species in the burn (7 % of detections) after Dark-eyed Junco (20.3 %), American Robin (13 %), Pine Siskin (9.3 %) and Yellow-rumped Warbler (7.6 %) in the seventh year post-fire. Because of the Mountain Bluebird's preference for open habitats, it appears to be strongly associated with fire and may be an indicator species with respect to the availability of younger age class habitats. In recent years, the Mountain Bluebird is not commonly seen in Kootenay National Park. During the biophysical inventory of Kootenay National Park (Poll et al. 1984), over 600 variable circular plots (representing over 100 hours of observation) were surveyed for birds. During this biophysical inventory there were only three sightings of Mountain Bluebirds. The absence of Mountain Bluebirds in my study may indicate the lack of suitable habitat. The Northern Hawk-Owl is another species strongly associated with early successional habitats (Poll et al. 1984). Due to its larger size and its predatory habit the Northern Hawk-Owl requires larger habitat patches than does the Mountain Bluebird and thus may be more adversely affected by lack of suitable habitat.

The similarity of bird communities between consecutive successional stages increases from earliest to latest stages with the herb-shrub stage being quite distinct from the older stages (Table 3). This distinctiveness of the bird community in the herb-shrub stage may be related to the pace at which vegetation succession occurs. During the first 50 years post-fire the stand changes from a herb-shrub to a closed canopy forest. After 50 years post-fire, once the canopy is formed, structural differences are less and structural changes proceed at a slower rate as the forest proceeds to climax (300 to 400 years post-fire).

Unlike outside national parks where the battle to save old growth forest lands from alteration continues to rage (Harris 1984), the problem wildlife managers face within our national parks is one of allowing disturbance such as naturally occurring fire. These disturbances must be allowed to occur if objectives of perpetuating naturally occurring vegetation patterns and consequently naturally occurring plant and animal communities are to be met. Begon et al. (1986) described the importance of disturbance as follows: "Just as the recurrent disturbances of the ice ages appear to have been powerful forces in the origin of species diversity, so the creation of gaps, new successions, and patchwork mosaics within communities may be the most powerful way in which we might generate and maintain ecological diversity."

CHAPTER 3

BIRD COMMUNITIES AND FOREST STRUCTURE

Many researchers investigating bird community-vegetation interactions in relation to forest succession report that bird diversity and abundance increase with successional age of the forest (Johnston and Odum 1956, Haapanen 1965, Anderson 1972, Shugart and James 1973, Meslow and Wight 1975, Shugart et al. 1978, Helle 1985). Shugart et al. (1978) suggest that this increase is associated with development of diverse vegetation structure which can be broadly equated to forest succession. As succession progresses, biomass increases and vegetation structure becomes more complex. These changes create more available niches and result in increased bird species diversity (Meslow 1978).

Balda (1975) noted that bird communities are the result of evolution of plants, which supply life requisites to birds, and birds, which must be efficient harvesters of these requisites. Structural components of the vegetation have utility in predicting bird community characteristics such as abundance, species richness and bird species diversity. Balda (1975) suggested that canopy height is the best factor upon which to make these predictions but concluded that percent cover and foliage volume should also be considered. In an attempt to identify factors accounting for bird species diversity in selected forest types, MacArthur and MacArthur (1961) found that the layering of vegetation alone could predict the number of breeding bird species in a temperate deciduous forest. Results of their work are supported by studies in different regions and habitats (Orians 1969, Recher 1969, Cody 1974). However, other studies (Balda 1969, Willson 1974, Wiens and Rotenberry 1981) do not support the foliage profile hypothesis proposed by MacArthur and MacArthur (1961).

In addition to having utility in predicting broad bird community characteristics, vegetation structure corresponds with the occurrence of particular bird species as well as guilds of species. A guild is a "group of species that exploits the same class of environmental resources in a similar way" (Root 1967). Most researchers have defined guilds according to foraging behaviour. Of more than 50 papers reviewed by Verner (1984) all but four described foraging guilds, yet patterns of species occurrence may be influenced by life requisites other than food. An obvious life requisite is nesting habitat because wildlife species are individually adapted to their habitats for both feeding and reproduction (Meslow and Wight 1975).

The purpose of my study was to examine relationships between bird communities and vegetation structure during forest succession in the subalpine zone of the Kootenay National Park, British Columbia. My objectives were to 1) examine relationships between bird community characteristics and broad structural attributes of vegetation, and 2) determine if the occurrence of nesting and feeding guilds of birds is related to vegetation structure.

METHODS

Choice of Successional Stages

Before going into the field, potential census areas at which to sample successional stages in the Lower Subalpine portion of the Subalpine Ecoregion were located on a 1:50,000 fire history map of Kootenay National Park (Masters 1989). Potential census areas were then previewed in the field. Three of the census areas chosen were within Kootenay National Park, one was located on the Banff National Park side of the Continental Divide and the last was located just outside the western boundary of Kootenay National Park. Five successional stages were identified: 1) herb-shrub, 2) pole-sapling, 3) young forest, 4) mature forest and 5) old growth forest (3, 21, 65, 163 and 241 years post-fire respectively)(Table 5). Because there have not been any recent large fires in the Lower Subalpine of Kootenay National Park, clearcuts outside the park boundary were used to represent an herb-shrub successional stage. The pole-sapling stand originated as a result of a forest fire in 1968 and is almost exclusively pole sized lodgepole pine. Because no homogeneous stands of lodgepole pine in young successional stages (approximately 65 years old) occur in the Lower Subalpine of Kootenay National Park, a site in Banff National Park was used. The mature successional stage is common in the Lower Subalpine of Kootenay National Park and is comprised of mixed lodgepole pine, Engelmann spruce, and subalpine fir approximately 150 years of age. The old growth stage originates from wildfire in the mid 1700's and is comprised of almost

Table 5. Mean values of vegetation and bird community characteristics (± SE) in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, 1989-90.

		Successional stage				
	Mnemonic	Herb-shrub	Pole-sapling	Young	Mature	Old growth
Vegetation Characteristics						
Canopy height[a]	CHGT	0.7 ± 0.0	4.1 ± 0.1	13.7 ± 0.2	22.1 ± 0.4	23.2 ± 0.2
Herb cover[b]	HCOV	30.0 ± 3.2	77.9 ± 2.3	43.2 ± 2.8	55.4 ± 2.7	52.6 ± 2.2
Low shrub cover[c]	LSCOV	11.9 ± 1.9	37.3 ± 2.1	31.3 ± 2.2	26.5 ± 2.0	36.7 ± 1.9
High shrub cover[d]	HSCOV	2.2 ± 0.9	23.3 ± 1.8	17.1 ± 1.8	30.9 ± 2.7	46.2 ± 2.7
Main canopy cover[e]	MCLO	0.0	0.0	39.2 ± 3.2	14.4 ± 2.1	10.9 ± 2.2
High canopy cover[f]	HCLO	0.0	0.0	0.7 ± 0.5	15.1 ± 2.2	17.6 ± 2.6
Total canopy cover[g]	TCLO	0.0	0.0	39.9 ± 3.1	29.5 ± 2.4	28.5 ± 2.8
Total cover[h]	TCOV	44.1 ± 5.0	138.5 ± 5.0	132.2 ± 5.5	157.4 ± 6.9	181.6 ± 7.1
Coniferous tree volume[i]	TVOL	0.0	28.6 ± 2.3	72.4 ± 7.6	80.2 ± 8.8	153.2 ±15.7
Lodgepole pine volume	LPVOL	0.0	28.6 ± 2.3	54.4 ± 6.6	23.3 ± 4.4	7.9 ± 3.3
Engelmann spruce volume	SPVOL	0.0	0.0	16.6 ± 6.2	54.3 ± 8.2	133.1 ±15.5
Subalpine fir volume	SFVOL	0.0	0.0	1.3 ± 1.0	2.6 ± 1.3	12.2 ± 3.9
Solid snags + stumps / ha	SNAGS	2.4 ± 0.6	3.7 ± 0.4	0.2 ± 0.1	2.4 ± 0.5	0.9 ± 0.3
Decaying snags + stumps / ha	SNAGD	0.1 ± 0.1	1.5 ± 0.4	0.3 ± 0.1	1.0 ± 0.2	1.7 ± 0.2
Punky snags + stumps / ha	SNAGP	0.0	0.0	1.8 ± 0.5	0.2 ± 0.1	0.1 ± 0.0
Total snags + stumps / ha	SNAG	2.5 ± 0.6	5.2 ± 0.5	2.3 ± 0.5	3.6 ± 0.6	2.7 ± 0.4
Foliage height diversity/plot	FHD	0.47 ±0.06	0.92 ±0.02	1.21 ±0.02	1.31 ±0.03	1.36 ±0.02
Tree species diversity/plot	TSD	0.00	0.00	0.07 ±0.05	0.31 ±0.05	0.18 ±0.04
Number of vegetation plots		40	72	60	64	68

Bird Community Characteristics						
Bird Community Indices						
Bird density[j]	BIRD	54.9 ± 7.5	115.8 ± 4.2	95.6 ± 5.5	202.0 ± 7.2	195.5 ± 9.0
Species richness/plot	SPEC	1.8 ± 0.2	4.4 ± 0.2	3.6 ± 0.2	5.8 ± 0.2	5.7 ± 0.3
Bird diversity/plot	BSD	0.27 ±0.06	1.28 ±0.05	1.14 ±0.07	1.44 ±0.05	1.45 ±0.06
Feeding Guilds[j]						
Air sallyer	SALL	6.5 ± 1.6	13.6 ± 2.8	1.3 ± 0.6	2.0 ± 0.6	3.5 ± 1.1
Bark gleaner	BAGL	0.0	1.1 ± 0.6	0.9 ± 0.5	9.4 ± 1.9	11.2 ± 3.2
Ground gleaner	GRGL	0.0	10.6 ± 1.8	8.6 ± 1.8	10.5 ± 2.0	15.6 ± 2.0
Ground forager	GRFO	46.9 ± 6.3	49.8 ± 3.5	21.0 ± 3.0	48.1 ± 5.9	45.2 ± 4.6
Canopy gleaner	CAGL	0.0	34.3 ± 2.2	60.4 ± 5.2	121.7 ± 7.3	111.5 ± 8.0
Canopy forager	CAFO	0.0	0.8 ± 0.4	2.8 ± 1.1	2.3 ± 0.9	2.7 ± 1.0
Nesting Guilds[j]						
Cavity nesters	CAVI	0.0	4.2 ± 1.1	7.0 ± 1.5	20.5 ± 2.5	22.7 ± 5.3
Ground nesters	GRND	49.5 ± 7.8	56.8 ± 4.4	13.3 ± 2.3	27.7 ± 4.1	40.0 ± 3.2
Shrub nesters	SHRB	0.0	24.3 ± 2.0	10.8 ± 2.1	19.8 ± 2.0	19.9 ± 2.8
Tree canopy nesters	TREE	3.9 ± 1.7	25.2 ± 3.6	64.8 ± 5.9	130.0 ± 7.3	111.9 ± 7.4
Number of bird plots		9	18	15	16	17

[a] Canopy height = height of dominant trees or bushes (m)
[b] Herb cover = total percent foliage cover in the 0.0 - 0.5 m layer
[c] Low shrub cover = total percent foliage cover in the 0.5 - 1.0 m layer
[d] High shrub cover = total percent foliage cover in the 1.0 - 10.0 m layer
[e] Main canopy cover = percent canopy closure in the 10.0 - 20.0 m layer
[f] High canopy cover = percent canopy closure > 20.0 m
[g] Total canopy cover = e + f
[h] Total cover = b + c + d + g (maximum possible = 500 %)
[i] Volumes are m^3 X 1000
[j] Density = number of individuals/40 ha

exclusively Engelmann spruce and subalpine fir. All five successional stages that I censused are in the Lower Subalpine at elevations between 1500 and 1700 m.

Bird Censuses

Birds were inventoried using the variable circular plot method (Reynolds et al. 1980). Within each successional stage, transects were located on aerial photographs then established on the ground. From about 0.5 hours before sunrise until 10:00 am MDT, plots were sampled along the transects at sites 200 m apart. In 1989, 9 plots were established in herb-shrub and 10 plots in each of the other stages. In 1990, 5 of the 10 plots sampled during 1989 in the pole-sapling, young, mature and the old growth stages were resurveyed. In addition to these plots, 8, 5, 6 and 7 new plots were surveyed in the pole-sapling, young, mature and old growth stages respectively. During 1989 and 1990 combined, 75 different circular bird plots were established. At the centre of each plot, I remained stationary for one minute before beginning to record bird activity for a 10 minute period. Each bird seen or heard was identified to species and recorded on a field sheet. The circular plot was divided into 10 m intervals of radius out to 100 m and the distance to each bird, at the location it was first seen or heard, was estimated and plotted on a field sheet. I also recorded species detected between 100 m and 250 m. Each record was noted as being visual, song, call, or an overflight. Most plots were censused 4 times within a field season. All censuses were conducted between 1 June and 30 June in both years. I conducted all the censuses to eliminate inter-observer bias.

Calculation of Bird Densities

Because of differences in vegetative structure among successional stages an effective detection distance should be determined for each species in each successional stage. I determined effective detection distances for all bird species detected a minimum of 20 times within a successional stage over the entire sampling period. Of the 28 detection distances calculated, 25 (89%) were 90 m or greater. Only 4 species were abundant enough to calculate detection distances across three or more successional stages. Of these 4 species, 3 had equal detection distances in all stages while the fourth had 3 detection distance radii of 100 m and 1 of 90 m. I concluded that under these conditions use of the 100 m detection distance radius for all species, rather than adjusted radii, was suitable for estimating densities (see also Finch and Reynolds 1987, Raphael 1987, Moskat and Szekely 1989). Following Franzreb (1976), when calculating densities, I used either the sum of all songs, calls and visual sightings of a species or the number of songs times 2 (to account for the mate of the territorial male), whichever was greater.

Treatment of Bird Data

For each 100 m radius plot, I totalled the number of individuals as well as the number of species detected (species richness, S). Bird species diversity/plot (H) was then calculated. I used the average of four counts at each plot for my estimates of bird density, species richness and diversity. Bird species diversity was calculated using the Shannon-Weaver (Shannon and Weaver 1949) diversity index:

$$H = - \Sigma p_i \log_e p_i$$

where p_i is the proportion of species i of the total number of individuals in the plot. Bird species equitability (J) was calculated using:

$$J = H/\log_e S$$

where S is species richness. Densities of flocking species such as Pine Siskins and White-winged Crossbills were not calculated and were not used in calculations of diversity. Birds were classified into foraging guilds following De Graaf et al. (1985) and nesting guilds following Ehrlich et al. (1983).

Vegetation Analysis

Four vegetation plots, 4.5 m in radius, were sampled at 50 m intervals across the diameter of each circular bird plot. For each vegetation plot, percent cover was estimated for five vegetation layers: 0.0-0.5 m, >0.5-1.0 m, >1.0-10.0 m, >10.0-20.0 m, >20.0 m. Foliage height diversity was calculated using the Shannon-Weaver index; where p_i = percent herb cover, percent low shrub cover, percent high shrub cover, percent main canopy closure or percent high canopy closure. Total cover was the sum of all five vegetation layers. Tree species diversity was calculated using the Shannon-Weaver index; where p_i = percent lodgepole pine canopy closure, percent Engelmann spruce canopy closure or percent subalpine fir canopy closure. Crown depth of one representative tree, of each tree species present, was measured. Using crown depth and percent canopy closure, crown volume was calculated for each tree species. At every second plot, snags and stumps were assessed and species, height, DBH and decay class (solid, decaying or punky) were noted. In addition, at every second plot, numbers of both downed trees and trees with dead tops were counted.

Bird-Vegetation Analyses

To investigate relationships between bird community characteristics and broad attributes of vegetation structure, I first used simple linear regressions. The vegetation variables used were chosen based on their biological importance and results from other studies. I then did multiple linear regressions, using the best predictors determined from the simple linear regressions, to estimate how much more of the variation in the bird community variables could be accounted for by additional vegetation structure variables. Before selecting variables for multiple regression analysis, Pearson correlation coefficients were calculated on all pairs of vegetation variables. All plots from all successional stages ($n = 304$) were included in the calculations. Highly correlated variables were excluded from the multiple regression analysis by including only one of every pair of variables with correlation coefficients > 0.70 (Noon 1981, Mannan and Meslow 1984).

RESULTS

Bird species encountered during bird censuses in each successional stage are listed in Table 2. Mean values of variables characterizing the structure and composition of vegetation as well as bird communities in the five successional stages censused are shown in Table 5. For analyses examining the relationships between bird variables and habitat variables, I used data pooled between years. Scientific names and guild designations of all bird species encountered during the study are listed in Appendix I.

Bird Community-Vegetation Structure Relationships

To investigate relationships between vegetation structure and bird community indices (bird density, species richness and diversity), six vegetation variables which I felt represented broad structural attributes of the vegetation, were chosen for regression analysis: foliage height diversity (FHD), height of dominant trees or shrubs (canopy height, CHGT), total percent vegetation cover (TCOV), percent main canopy closure (MCLO), conifer volume (TVOL) and tree species diversity (TSD). Pearson correlation coefficients among these vegetation variables are shown in Table 6.

Results of simple linear regressions (r^2 values) of bird community indices (bird density, species richness/plot and bird

Table 6. Pearson correlation coefficients for variables characterizing the structure and composition of vegetation in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, 1989-1990. All correlations are significant ($P < 0.05$). FHD = foliage height diversity/plot, CHGT = height of dominant trees or shrubs (canopy height), TCOV = total percent vegetation cover, MCLO = percent main canopy closure, TVOL = coniferous tree volume, TSD = tree species diversity.

	Vegetation Variables				
	FHD	CHGT	TCOV	MCLO	TVOL
CHGT	0.75				
TCOV	0.71	0.51			
MCLO	0.27	0.25	0.12		
TVOL	0.57	0.54	0.62	0.36	
TSD	0.37	0.42	0.23	0.14	0.26

diversity/plot) against vegetation variables are presented in Table 7. Because the herb-shrub and pole-sapling stages do not have a well developed coniferous tree canopy, structural attributes of vegetation in these earliest successional stages are quite distinct from the three oldest stages. To examine the breadth of bird community-vegetation structure relationships, I did analyses using all five successional stages (ALL) as well as only the three oldest successional stages (MAT).

Bird Density

Canopy height (CHGT) was the single variable which accounted for the greatest amount of variation in bird density when all successional stages were included ($r^2 = 0.62$) as well as when data from only the three oldest successional stages were used ($r^2 = 0.65$). Using data from all successional stages, the inclusion of total percent vegetation cover (TCOV) as a second independent variable (bird density = Constant + CHGT + TCOV) accounted for only an additional 3 % ($P < 0.05$) of the variation in density of birds ($R^2 = 0.65$). These relationships are expressed graphically (Fig. 6) using a distance weighted least squares smoothing function (Systat 1989). The inclusion of other variables did not significantly improve the relationship that I found using canopy height alone. When only the three oldest successional stages were considered, inclusion of total conifer volume (TVOL) as a second independent variable (bird density = constant + CHGT + TVOL)

Table 7. Results of simple linear regressions (r^2 values) of bird community indices: bird density, species richness/plot, and bird diversity/plot against selected variables characterizing the structure and composition of vegetation in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, during the breeding season, 1989-90.

	FHD[a]		CHGT		TCOV		MCLO		TVOL		TSD	
	ALL[b]	MAT[c]	ALL	MAT	ALL	MAT	ALL	MAT	ALL	MAT	ALL	MAT
Bird density	0.45*	0.15*	0.62*	0.65*	0.40*	0.18*	0.00	0.46*	0.33*	0.07	0.33*	0.17*
Bird diversity/plot	0.47*	0.06	0.36*	0.27*	0.49*	0.06	0.01	0.20*	0.22*	0.02	0.15*	0.11*
Species richness/plot	0.42*	0.16*	0.44*	0.47*	0.43*	0.14*	0.00	0.34*	0.23*	0.03	0.27*	0.20*

[a] refer to Table 5 and text for description and mnemonics of variables
[b] data from all successional stages used in regressions
[c] data from only the three oldest successional stages used in regressions
* significant, $P < 0.05$

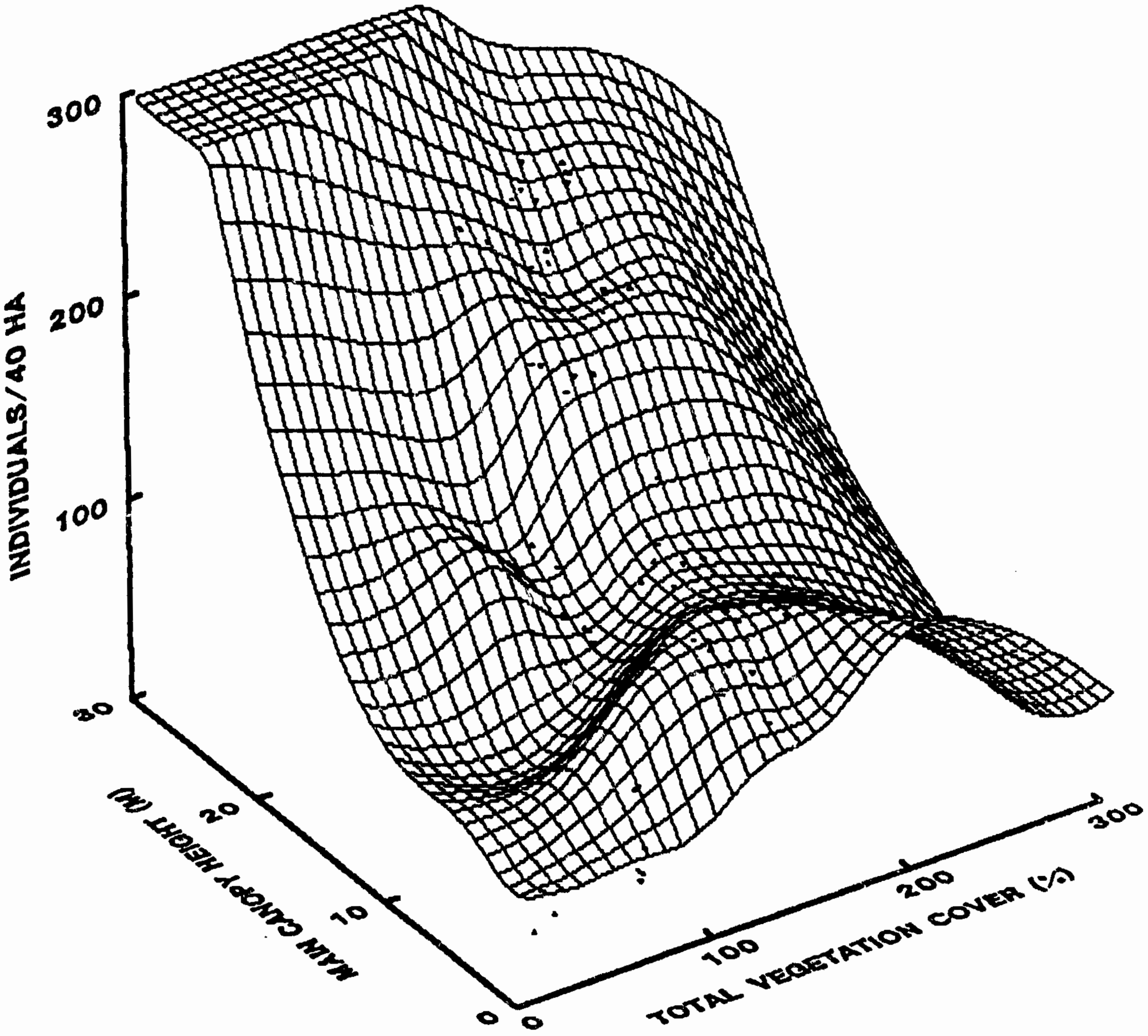

Figure 6. Three dimensional plot of mean bird density (individuals/40 ha) versus main canopy height (m) versus total percent vegetation cover (maximum possible = 500 percent).

increased the amount of variation accounted for by less than 1 % ($R^2 = 0.65$, $P < 0.05$).

Species Richness

Canopy height was the single variable which accounted for the greatest amount of variation in species richness/plot when all successional stages were considered ($r^2 = 0.44$) as well as when data from only the three oldest successional stages were used ($r^2 = 0.47$). Using data from all successional stages, the inclusion of total percent vegetation cover (TCOV) as a second independent variable (species richness/plot = constant + CHGT + TCOV) accounted for an additional 8 % ($P < 0.05$) of the variability of species richness/plot ($R^2 = 0.52$). Using data from only the three oldest successional stages, the inclusion of additional vegetation variables in multiple linear regressions did not significantly increase the amount of variation in species richness/plot accounted for by canopy height alone ($P > 0.05$).

Bird Diversity

Total percent vegetation cover was the best predictor of bird diversity/plot ($r^2 = 0.49$) when all successional stages were included in the analysis but when data from only the three oldest stages were used, canopy height accounted for the greatest amount of the variation in bird diversity/plot ($r^2 = 0.27$). Using all successional stages, the inclusion of canopy height as a second independent variable (bird diversity/plot = constant + TCOV +

CHGT) accounted for only an additional 3 % ($P < 0.05$) of the variation in bird diversity/plot ($r^2 = 0.52$). Using data from only the three oldest successional stages, the inclusion of additional vegetation variables in multiple linear regressions did not significantly increase the amount of variation in bird diversity/plot that was accounted for by main canopy height alone ($P > 0.05$).

I found a strong positive relationship between bird diversity/plot and foliage height diversity/plot (Fig. 7) when all successional stages were included in the analysis ($r^2 = 0.47$, $P < 0.05$) but not when data from the youngest successional stages were excluded ($r^2 = 0.06$, $P > 0.05$).

Bird Guild-Vegetation Structure Relationships

Rather than regressing all guild densities on all possible vegetation variables, I selected vegetation variables a priori, based on a knowledge of nesting and feeding requirements of birds, that I felt had biological utility in predicting occurrence of guilds (Table 8). There was no relationship between the density of cavity nesting birds and the total density of solid snags and stumps or total density of decaying snags regardless of whether data from all five successional stages or only the three oldest stages were used. There was a positive relationship ($P < 0.05$) between the density of cavity nesters and the density of soft (decaying or punky), non-spruce (lodgepole pine or subalpine fir) snags and stumps. There was also a positive relationship between

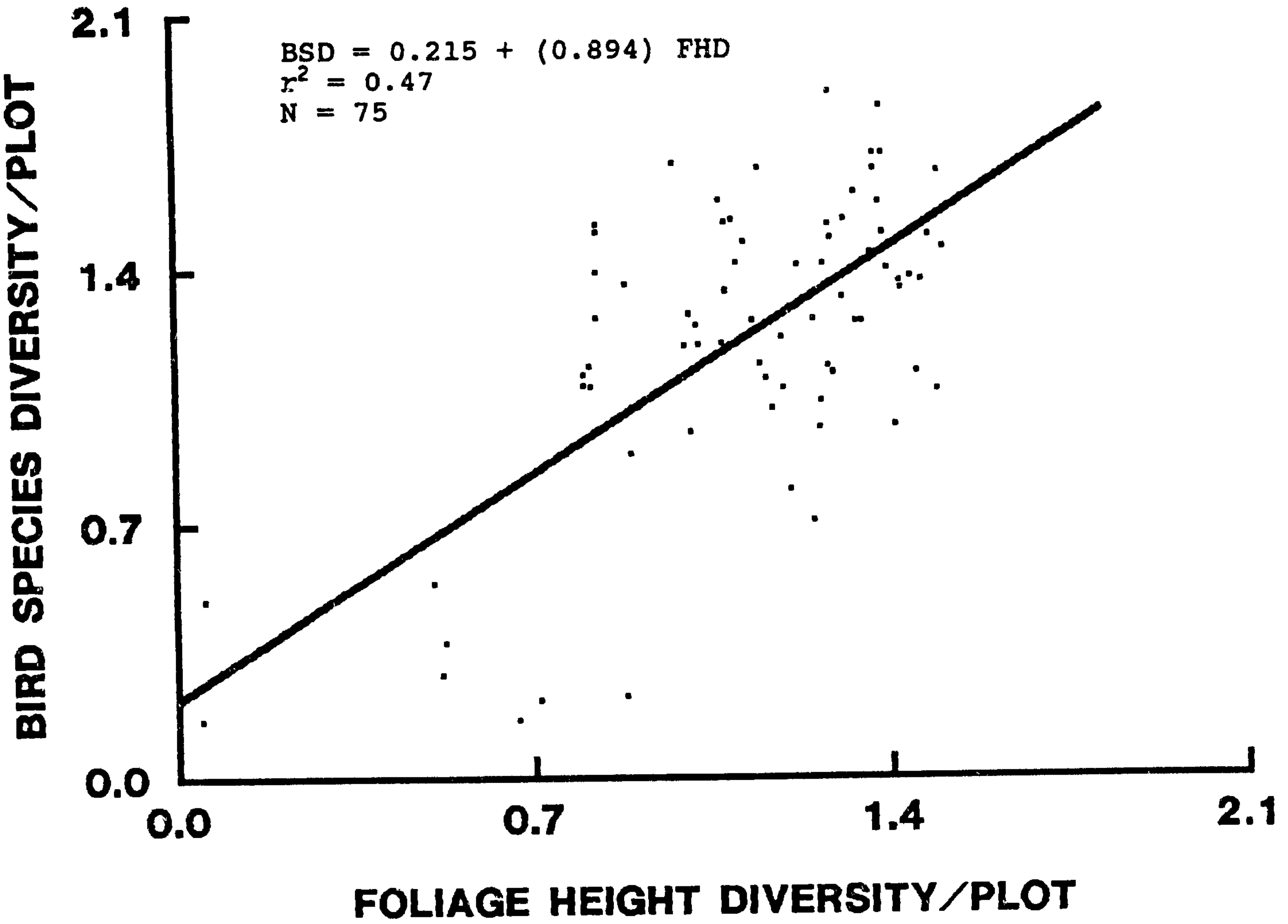

Figure 7. Bird diversity/plot and foliage height diversity/plot in the Lower Subalpine of Kootenay and Banff National Parks, 1989-1990. Data include all vegetation plots from all five successional stages.

Table 8: Results of linear regressions (r^2 values) of densities for selected foraging and nesting guilds with variables characterizing the structure and composition of vegetation in the Lower Subalpine of Kootenay and Banff National Parks. For all reported relationships slopes are positive.

Guild	Vegetation Variable[a]	ALL[b]		MAT[c]	
		r^2	P[d]	r^2	P
Nesting Guild					
Cavity nester	SNAG	0.01	ns	0.01	ns
Cavity nester	SNAGS	0.02	ns	0.02	ns
Cavity nester	SNAGD	0.02	ns	0.06	ns
Shrub nester	HSCOV	0.20	***	0.17	**
Ground nester	HCOV	0.11	**	0.02	ns
Tree canopy nester	CHGT	0.78	***	0.40	***
Tree canopy nester	TVOL	0.38	***	0.01	ns
Tree canopy nester	TCOV	0.38	***	0.05	ns
Feeding Guild					
Air sallyer	SNAG	0.08	*	0.03	ns
Air sallyer	SNAGS	0.16	**	0.00	ns
Air sallyer	SNAGD	0.00	ns	0.10	*
Canopy gleaner	CHGT	0.76	***	0.44	***
Canopy gleaner	TVOL	0.41	***	0.04	ns
Canopy gleaner	TCOV	0.35	***	0.04	ns

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[a] descriptions of habitat variables are given in Table 5

[b] all successional stages used in analyses

[c] only the three oldest successional stages used in analyses

[d] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant

the density of cavity nesters and the numbers of trees with dead tops (Spearman rank correlation, $r_s = 0.32$, $P < 0.05$). Because I often saw flycatchers perched on tops of snags, I hypothesized that snags were an important habitat feature to this guild. Using data from all successional stages, density of air sallyers was related to total density of snags and stumps ($P < 0.05$) but not when only decaying snags and stumps were considered ($P > 0.05$). When only the three oldest stages were used in my analysis, density of air sallyers was related only to density of decaying snags and stumps ($P < 0.05$).

Density of ground nesters was related to percent cover of vegetation in the 0 - 0.5 m (HCOV) layer when all successional stages were included ($P < 0.05$) but not when the two youngest stages were excluded from the analysis ($P > 0.05$). Using data from all successional stages, inclusion of the percent cover of the > 0.5 - 1.0 m vegetation layer (LSCOV) as a second independent variable (ground nesters = constant + HCOV + LSCOV) accounted for an additional 9 % ($P < 0.05$) of the variation in the density of ground nesters.

Density of the guild which typically nests in shrubs was significantly related to percent cover of the > 1 - 10 m layer of vegetation (HSCOV) when all successional stages were included in the analysis as well as when only the three oldest stages were considered ($P < 0.05$). Using data from all successional stages, inclusion of percent cover of the 0.0 - 0.05 m vegetation layer (HCOV) as a second independent variable (shrub nesters = constant

+ HSCOV + HCOV) accounted for an additional 18 % ($P < 0.05$) of the variation in density of shrub nesters ($r^2 = 0.38$). When only the three oldest stages were considered, inclusion of percent cover of the 0.0 - 0.5 m vegetation layer did not significantly improve the relationship ($P > 0.05$).

There was a strong relationship between canopy height and density of canopy gleaning (CAGL) species ($r^2 = 0.76$, $P < 0.05$) and canopy nesting (TREE) species ($r^2 = 0.78$, $P < 0.05$) when all successional stages were used as well as when only the three oldest successional stages were considered (CAGL, $r^2 = 0.44$, $P < 0.05$; TREE, $r^2 = 0.40$, $P < 0.05$). Similar relationships between vegetation structure and these two guilds was expected because densities of these guilds were highly correlated ($r = 0.91$, $P < 0.05$). Using data from all successional stages, inclusion of conifer volume (TVOL) (canopy nesters = constant + CHGT + TVOL) increased the amount of variation accounted for in density of canopy nesters by just 1 % and the variation accounted for in the density of canopy gleaners (canopy gleaners = constant + CHGT + TVOL) by less than 1 %. When only the mature stages were considered, the inclusion of conifer volume (TVOL) (canopy nesters = constant + CHGT + TVOL) accounted for an additional 5 % of the variation in the density of canopy nesters than when canopy height was used alone. Percent total canopy closure (TCLO) and total conifer volume (TVOL) were single variables that also accounted for a high proportion of the variation in densities of canopy nesters (TCLO, $r^2 = 0.38$; TVOL, $r^2 = 0.38$) as well as canopy gleaners (TCLO, $r^2 = 0.35$; TVOL, $r^2 = 0.41$) when all successional stages were included in the analysis. These vegetation variables did not have a significant effect on canopy nesting or canopy foraging guilds when only the three oldest successional stages were considered.

DISCUSSION

Many studies have examined the relationship between bird species diversity and foliage height diversity since MacArthur and MacArthur (1961) first proposed the foliage profile hypothesis. When data from all successional stages were used, I found strong, positive relationships between bird community indices and foliage height diversity/plot (FHD) (Fig. 7), main canopy height (CHGT) and total percent vegetation cover (TCOV) (Table 4). When structurally different early successional stages were excluded from my analysis, the predictive value of foliage height diversity/plot was reduced substantially while that of canopy height increased slightly (Table 7). I found similar relationships between bird density and foliage height diversity. When all successional stages were considered foliage height diversity/plot was the second best predictor of bird density but when data from the early successional stages were removed, strength of the bird density-foliage height diversity/plot relationship dropped. Similar results have been reported by Willson (1974) and Erdelen (1984). Both authors found that the bird species diversity-foliage height diversity relationship held true only when data from structurally dissimilar habitats (i.e. field and forest) were used, but not when data from only forested plots were used. In Kootenay National Park, the amount of variation in bird density accounted for by canopy height stayed relatively constant regardless of whether all or only the three oldest successional stages were used.

Results of my study support those of Balda (1975) who suggested that height of dominant trees or shrubs (canopy height) was the best predictor of bird community indices such as bird density, species richness and diversity. I found that unlike foliage height diversity, which lost its predictive capability when structurally different habitats were excluded, the relationships between canopy height and bird community indices remained more or less the same when either all or only the three oldest successional stages were used.

My data support the original hypothesis of MacArthur and MacArthur (1961) in that vegetation structure is more closely related to bird species diversity than is floristic composition, here expressed as tree species diversity (TSD). I did find significant relationships between bird community indices and tree species diversity but they tended to be weaker (lower r^2) than those for foliage height diversity and canopy height. The relationships between tree species diversity and bird community indices were less sensitive to the absence of structurally different habitats (herb-shrub and pole-sapling) than was foliage height diversity.

Results from a study comparing bird indices in managed and unmanaged forests in Arizona (Franzreb and Ohmart 1978) indicate that the absolute amounts of vegetation (i.e. volume) may be important to birds. Their study compared unmanaged stands which had never been harvested with managed stands where approximately 70 % of the trees had recently been removed. Despite differences in basal area of trees, foliage height diversities were similar between the two study sites. Surprisingly, bird species diversities in the two study sites were also similar and thus the study seemed to support the foliage profile hypothesis. However, although bird species diversity was similar between their study sites, densities of birds were significantly higher in unmanaged stands. The total volume of vegetation in unmanaged stands was over seven times greater than that in the managed stands and this difference may explain differences in densities found in their two sites (Hunter 1990). In my study, multiple linear regression revealed that when canopy height was held constant, both total volume and total percent cover of coniferous trees accounted for significantly more of the variation in bird density than did canopy height alone, although the amount of additional variation accounted for was small.

Karr and Roth (1971) found a sigmoid relationship between bird species diversity and total percent vegetation cover. In my study the relationship between bird diversity/plot and total percent vegetation cover was positive and linear ($r^2 = 0.49$). Although I found a significant relationship between bird density and total percent vegetation cover using simple linear regression (Table 4), inspection of Figure 6 suggests that the relationship could be curvilinear (sigmoid) rather than linear. Karr and Roth (1971) suggested that the sigmoid relationship between bird species diversity and total percent vegetation cover indicates that birds are responding to the addition of vegetation layers. Inclusion of the grass layer contributes only slightly to bird diversity while the addition of shrubs followed by the addition of tree layers results in a peak rate of increase in bird diversity. They suggested a decrease in bird diversity after that point results from a restriction of mobility of birds in dense foliage.

Evidently, no one factor can be proposed as the sole determinant for bird community characteristics in forest habitats. Erdelen (1984) suggested that simpler indices of vegetation structure (e.g. canopy height, percent cover) should be used rather than complex ones (e.g. foliage height diversity). He points out that empirically simple indices are often closely correlated with complex ones (in my study the correlation between foliage height diversity and canopy height was high; $r = 0.75$, $P < 0.05$) and can therefore be substituted without much loss of information. He added that simpler indices can be better standardized and compared because they are easier to understand and interpret.

Parker (1987) reported that although, on a regional scale, relationships exist between guilds of birds species with similar feeding habits (foraging guilds) and gross vegetation structure, these types of relationships do not hold true for guilds of species with similar nesting habits (nesting guilds). Parker (1987) found instead that forest type was related to the nesting habits of species. In my study I examined relationships between guilds of species, both foraging and nesting, and gross vegetation structure at the scale of the forest stand. I found significant relationships between densities of many foraging and nesting guilds and structural features of the habitat.

Other studies considered bird species that are restricted by the limited availability of suitable nest substrates (Bull 1978). Snags are used by birds for nesting, feeding, perching and roosting (Bull 1978). Not all snags are alike in hardness and appearance. The condition (Bull 1978), size (Evans and Conner 1979), and tree species (Haapanen 1965, Harestad and Keisker 1989) of the snag, are all important in determining its suitability for use by cavity nesters.

I did not find a relationship between the density of cavity nesting birds and total density of snags and stumps. In the field, I counted only standing dead trees with a DBH of 10 cm or greater (Evans and Conner 1979) and a height of 0.75 m or taller (Schwab 1979) and I also noted their condition (solid, decaying or punky). I did not expect to find a relationship between density of cavity nesters and density of solid snags. In my study area the greatest densities of snags were in the pole-sapling stage (Table 2). The majority of these snags were fire killed Engelmann spruce with no bark remaining and little decayed heartwood. Raphael (1980) found nest trees of cavity nesters had significantly more bark than non-nest trees while Harestad and Keisker (1989) found heartwood decay the most important factor in nest tree selection by primary cavity nesting birds. I expected, but did not find, a positive correlation between the density of decaying snags and stumps and density of cavity nesters.

Perhaps species of snag may influence the occurrence of cavity nesters. In Kootenay National Park, the majority of snags present in the pole-sapling stage, as well as those in the old growth stage, were dead Engelmann spruce. Haapanen (1965) suggested that the best successional stage for cavity nesters is during the mixed stand phase (mature forest in my study area, with a mixture of lodgepole pine, Engelmann spruce and subalpine fir). He predicted that, because of the difficulty of cavity excavation in spruce, the number of cavity nesters would decrease as the forest changed to pure stands of spruce. Based on this rationale, I expected a relationship between density of soft, non-spruce snags and the density of cavity nesters. Cavity nesters were positively correlated (Pearson correlation, $r = 0.23$) to the densities of soft, non-spruce snags and stumps ($P < 0.05$). This relationship is significant, but weak, and it is difficult to say whether the weakness of the relationship is real or due to inadequate sampling of either snags or cavity nesters, or both. My estimates of snag densities seem low (Table 1) and censusing birds using point counts often give poor estimates of woodpecker densities (J.P. Savard personal communication).

It is important to note that not all variance in density and diversity of forest birds can be attributed to habitat factors. There are a number of biological factors that also play important roles. Included among these are competitive interactions, reduction in niche dimensions (increased specialization) and morphological adaptations. Nonetheless, my study has shown that structural components of vegetation have utility in predicting bird community characteristics such as abundance, species richness and diversity as well as the occurrence of suites of species categorized by both their feeding and nesting life requisites.

CHAPTER 4

BIRD COMMUNITIES AND FOREST EDGES

Thomas et al. (1978) defined an "edge" as the area where two or more plant communities, or successional stages within plant communities, meet and an "ecotone" as the area influenced by the transition between these communities or successional stages. Because of the intermixing of plant communities, edges and their associated ecotones are usually assumed to contain more species and more individuals than do homogeneous habitats on either side of the ecotone (Odum 1971). The resulting increased structural complexity along an edge provides life requisites that support greater numbers of species than do either habitat adjacent to the ecotone (Thomas et al. 1979a). The tendency for increased diversity and abundance at these community junctions is called "edge effect" (Odum 1971).

Thomas et al. (1978) described two types of edge. An inherent edge is a long-term condition caused by factors such as soil, topography, geomorphology, and microclimate. An induced edge is a short-term condition created by factors such as fire, disease, grazing and timber harvest. Edges can also differ in their degree of contrast. In a system with five successional stages (herb-shrub, pole-sapling, young, mature, and old growth), there are 10 possible combinations of edges, all with different degrees of contrast. For example, a herb-shrub stage and a pole-sapling stage have a low degree of contrast, whereas a herb-shrub stage and an old growth forest stage have a high degree of contrast.

Until recently, only a few studies had quantified the "edge effect" in regards to density and diversity of nongame birds (Strelke and Dickson 1980, Kroodsma 1982, Kroodsma 1984, Hansson 1983, Small and Hunter 1989). These studies have examined the effects of abrupt induced edges created by clearcuts (Strelke and Dickson 1980, Hansson 1983) and powerlines (Kroodsma 1982, Kroodsma 1984, Small and Hunter 1989), as well as abrupt inherent edges along forest-river interfaces (Small and Hunter 1989). No studies have examined the effects of fire induced edges on bird communities or the effects of edge contrast.

The purpose of my study was to examine relationships between bird communities and forest edges in the subalpine zone of Kootenay National Park, British Columbia. My objectives were to determine if bird density, species richness and bird species diversity at the edge between two successional stages are greater than those found in homogeneous interior of each adjacent successional stage. I also determine if these differences in density, richness and diversity at the edge between two different successional stages decrease as contrast between the two successional stages decreases.

METHODS

Choice of Edge Plots and Successional Stages

Before going into the field, edges between successional stages in the Lower Subalpine portion of the Subalpine Ecoregion were located on aerial photos. Potential study sites were then previewed in the field. A high contrast edge between pole-sapling and old growth stages (Vermilion River survey area) and a low contrast edge between mature and old growth stages (Helmet Creek survey area) were chosen. The pole-sapling stand originated as a result of a forest fire in 1968 and is almost exclusively pole sized lodgepole pine. The mature successional stage is common in the Lower Subalpine of Kootenay National Park and is comprised of mixed lodgepole pine, Engelmann spruce, and subalpine fir approximately 150 years of age. The two old growth stands (Vermilion River and Helmet Creek) originated from wildfire in the mid 1700's and are comprised of almost exclusively Engelmann spruce and subalpine fir. Both survey areas are in the Lower Subalpine at elevations between 1500 and 1700 m.

Bird Censuses

Birds were inventoried using the variable circular plot method (Reynolds et al. 1980). The amount of edge, terrain and unpredictable weather severely restricted the number of transects I could survey. In 1989, circular plots were surveyed along two transects perpendicular to the edge between pole-sapling and old growth successional stages (transects 1 and 2). Both transects were 2.2 km in length with five circular plots in homogeneous successional stages on either side of the edge plots (Fig. 8). All plots along transect 1 were surveyed again in 1990, but for transect 2, only the edge plots, and one interior plot on either

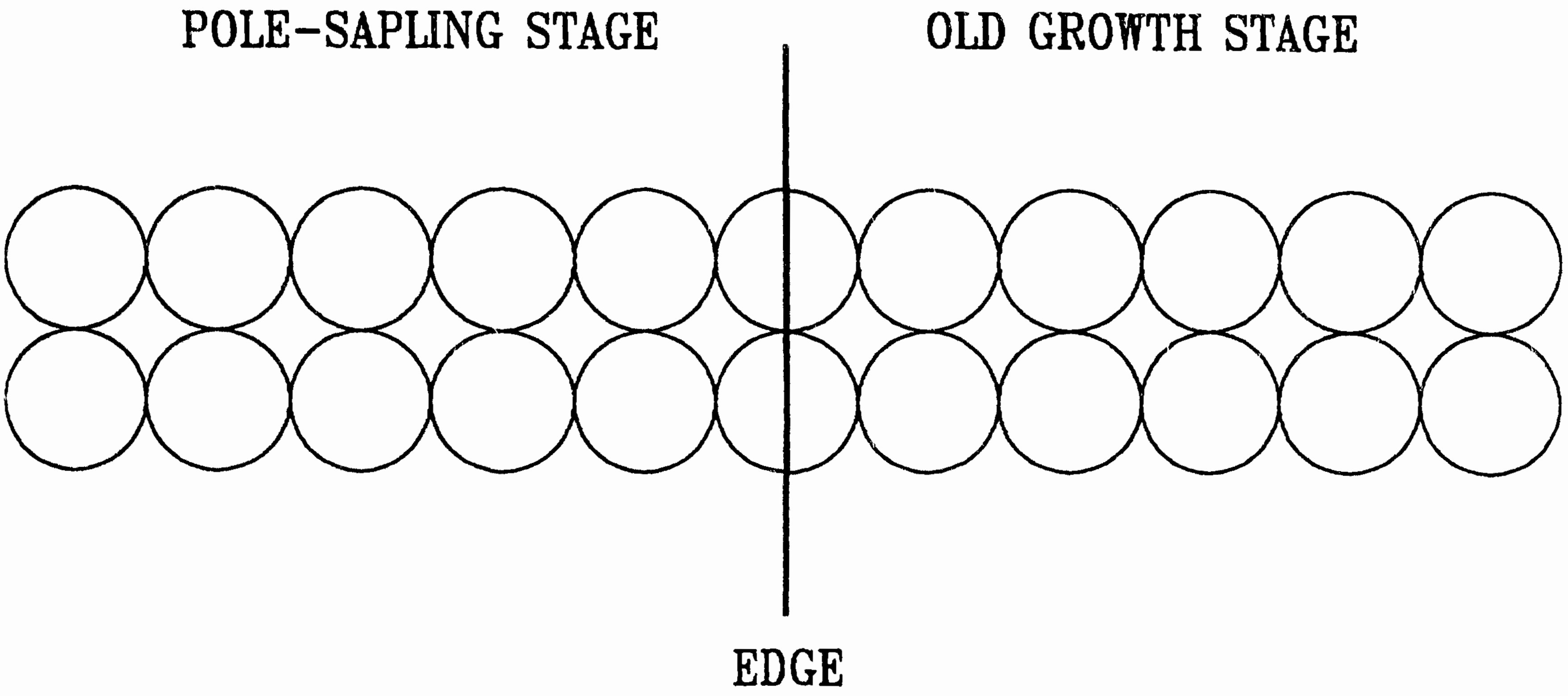

Figure 8. Location of circular bird plots across the edge between pole-sapling and old growth successional stages. Transect 3 across the edge between mature and old growth successional stages was set up in a similar fashion.

side of the edge, was surveyed again in 1990. In the 1990 field season, circular breeding bird plots were also conducted along one transect perpendicular to the edge between mature and old growth successional stages (transect 3). The middle plots in the three different transects were placed at the edge such that half of the plot was in the pole-sapling stage and half of the plot was in the old growth stage (transects 1 and 2) or half of the plot in the mature stage and half of the plot in the old growth stage (transect 3). Thus, four different contexts of edge were possible: 1) pole-sapling interior with pole-sapling edge plots adjacent to the old growth stage (Fig. 9, left side), 2) old growth interior with old growth edge plots adjacent to the pole-sapling stage (Fig. 9, right side), 3) mature interior with mature edge plots adjacent to the old growth successional stage (Fig. 10, left side) and 4) old growth interior with old growth edge plots adjacent to the mature stage (Fig. 10, right side). Points were sampled along the transects at sites 200 m apart from about 0.5 hours before sunrise until 10:00 am MDT. At the centre of each plot I remained stationary for one minute before beginning to record bird activity for a 10 minute period. Each bird seen or heard was identified to species and recorded on a field sheet. The circular plot was divided into 10 m intervals of radius out to 100 m and the distance to each bird, at the location it was first seen or heard, was estimated and plotted on a field sheet. Each record was noted as being visual, song, call, or an overflight.

The pole-sapling/old growth transects were censused 4 times

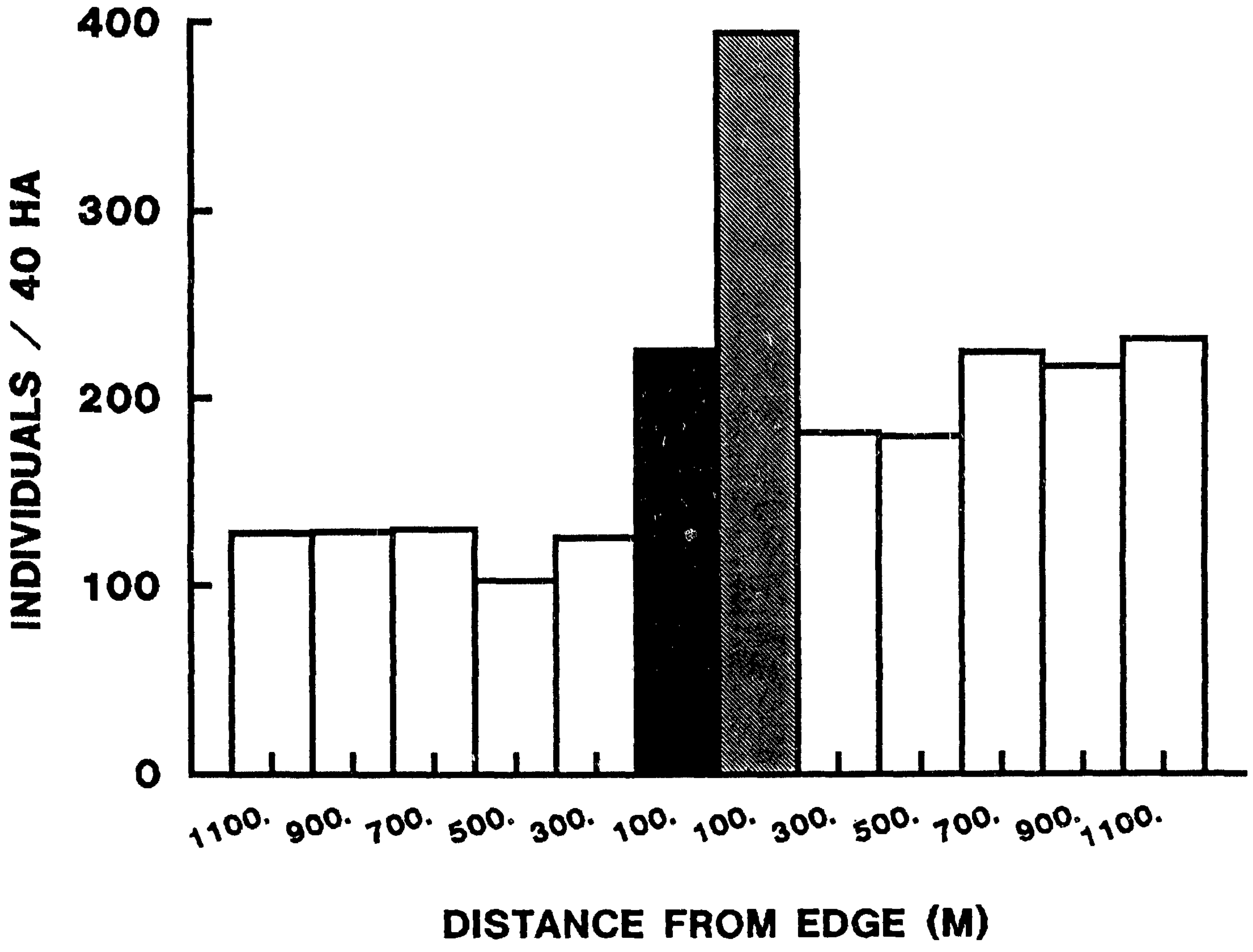

Figure 9. Bird density at different distances from the pole-sapling/old growth edge. Edge plot densities are shown in solid black (pole-sapling) and with cross hatching (old growth). White bars to the left of the edge plot densities represent densities in pole-sapling interior. White bars to the right of the edge plot densities represent densities in old growth interior.

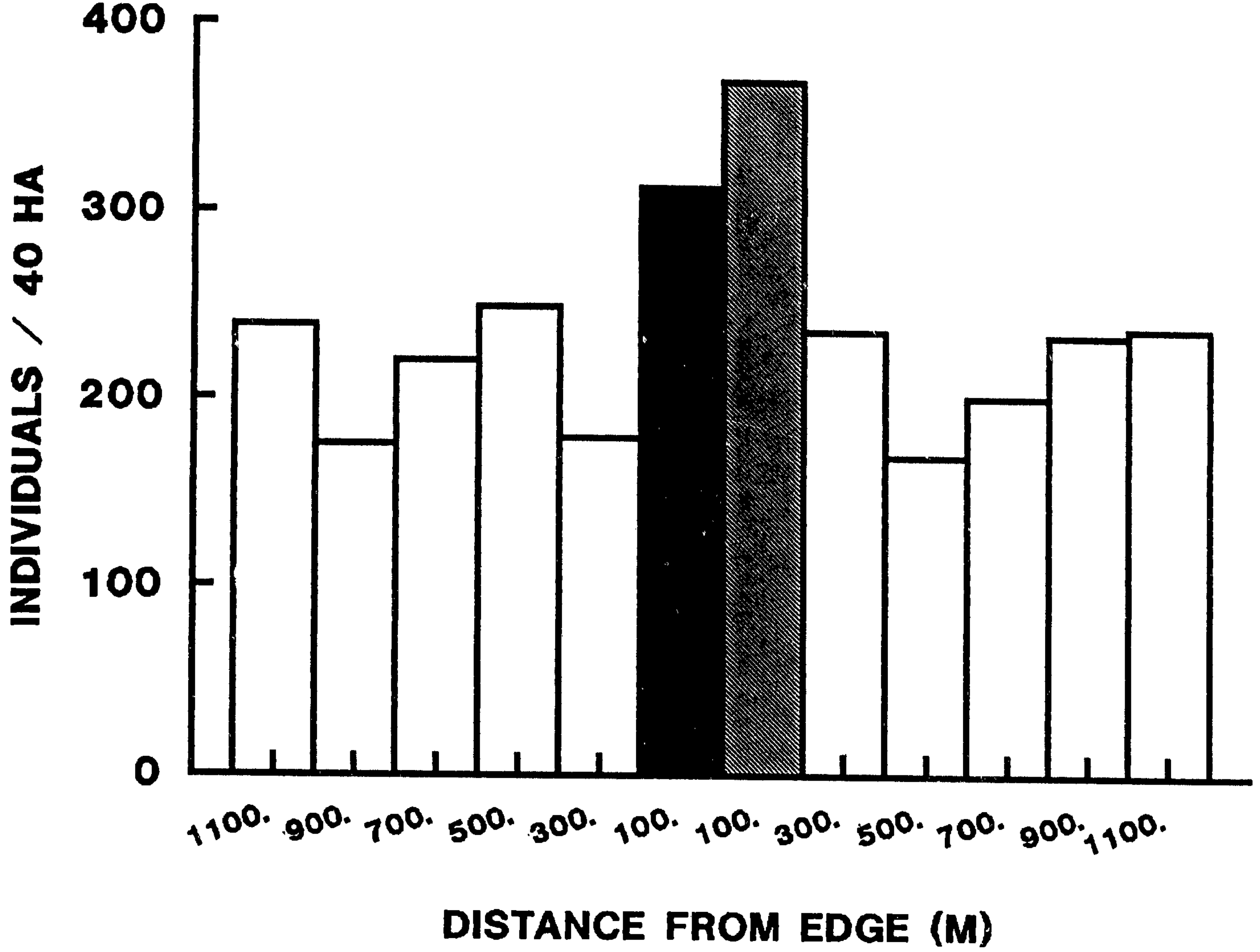

Figure 10. Bird density at different distances from the mature/old growth edge. Edge plot densities are shown in solid black (mature) and with cross hatching (old growth). White bars to the left of the edge plot densities represent densities in mature interior. White bars to the right of the edge plot densities represent densities in old growth interior.

in 1989 and 1990. In 1990 the mature/old growth transect was censused four times. All censuses were conducted between 1 June and 30 June in both years. I conducted all the bird censuses to eliminate interobserver bias.

Calculation of Bird Densities

Because of differences in vegetation structure among successional stages an effective detection distance should be determined for each species in each successional stage. I determined effective detection distances for all bird species detected a minimum of 20 times within a successional stage over the entire sampling period. Of the 22 detection distances calculated in the three successional stages, 19 (86%) were 90 m or greater. Only 3 species were abundant enough to calculate detection distances across three or more successional stages. Of these 3 species, 2 had equal detection distances in all stages while the third had 2 radii of 100 m and 1 of 90 m. I concluded that under these conditions use of the 100 m detection distance radius, for all species, rather than adjusted radii, was suitable for estimating densities (see also Finch and Reynolds 1987, Raphael 1987, and Moskat and Szekely 1989). Following Franzreb (1976), when calculating densities I used either the sum of all songs, calls and visual sightings of a species or the number of songs times 2 (to account for the mate of the territorial male), whichever was greater.

Treatment of Bird Data

For each 100 m radius plot, the number of individuals as well as number of species detected (species richness, S) were totalled and bird species diversity/plot (H) was calculated. In order to compare species richness at the edge with values in interior habitats I determined species richness/half plot for all plots from raw data. I used the average of four counts at each plot for my estimates of bird density, species richness and diversity. Bird species diversity was calculated using the Shannon-Weaver (Shannon and Weaver 1949) diversity index:

$$H = - \Sigma p_i \log_e p_i$$

where p_i is the proportion of species i of the total number of individuals in the plot. Densities of flocking species such as Pine Siskins and White-winged Crossbills were not calculated and not used in calculation of diversity.

I used linear regression to determine whether bird density, species richness and bird diversity were related to distance from the edge. Data from the edge plots (0 to 100 m from the edge), for each possible context of edge and for both years, were pooled and compared to values from interior plots (>100 to 1100 m) from the edge. Differences in density, species richness and diversity between edge and interior sites were tested by the Wilcoxon signed-ranks test.

Vegetation Analysis

Within each circular bird plot four vegetation plots, 4.5 m in radius, were sampled at 50 m intervals across the diameter of the plot. For each vegetation plot, percent cover was estimated for each of five layers: 0.0-0.5 m, >0.5-1.0 m, >1.0-10.0 m, >10.0-20.0 m, >20.0 m. Total cover was the sum of all five vegetation layers. Percent canopy closure of each tree species was estimated, and mean crown depth was measured, for each tree species present. Using crown depth and percent canopy cover of each tree species, crown volume for each species was calculated.

RESULTS

Vegetation Characteristics

Vegetation characteristics of both edge and interior portions of the three successional stages, in the two survey areas, are shown in Table 9. Vegetation in the pole-sapling stage was quite distinct from that of the old growth stage while that of the mature stage was very similar to that of the old growth stage. Vegetation characteristics of the edge plots were similar to those of their respective interior sites.

Bird Community Characteristics

Because of the possible bias resulting from using half plots to determine densities of species along the edge, I did a linear regression of mean half plot (h) densities with their respective mean full plot densities (f) (using data from both interior old growth and interior pole-sapling) to determine if full plot densities were comparable to half plot densities. The resulting

Table 9. Mean values of vegetation characteristics (± SE) in edge and interior plots of three successional stages at two study sites in the Lower Subalpine of Kootenay National Park, British Columbia.

	Study Site							
	Vermilion River				Helmet Creek			
	Pole-sapling		Old Growth		Mature		Old Growth	
	edge	interior	edge	interior	edge	interior	edge	interior
Canopy height[a]	3.8±0.2	3.8±0.9	22.3±0.3	22.8±0.3	21.3±0.7	21.9±0.6	24.3±0.9	24.0±0.4
Herb cover[b]	65.0±3.7	80.4±2.3	59.4±2.7	44.3±2.1	58.3±6.7	48.9±4.6	63.3±6.0	61.8±3.8
Low shrub cover[c]	34.4±3.1	28.1±1.8	50.0±3.7	31.8±1.9	48.3±7.3	21.9±3.8	55.0±2.9	42.9±4.7
High shrub cover[d]	13.8±2.3	14.7±1.2	34.4±3.1	44.5±3.5	28.3±3.3	36.7±5.6	57.0±5.7	51.4±5.2
Main canopy cover[e]	0.0	0.0	18.1±2.5	31.0±4.0	21.7±3.3	38.0±4.6	20.0±2.9	27.7±4.4
High canopy cover[f]	0.0	0.0	10.6±1.5	16.3±3.7	16.7±3.3	18.3±1.7	18.3±1.7	21.6±4.7
Total cover[g]	113.2	123.2	172.5	167.9	173.3	163.8	213.6	205.4
Number of plots	8	40	8	40	3	20	3	20

[a] Canopy height = height of dominant trees or bushes (m)

[b] Herb cover = total percent foliage cover in the 0.0 - 0.5 m layer

[c] Low shrub cover = total percent foliage cover in the 0.5 - 1.0 m layer

[d] High shrub cover = total percent foliage cover in the 1.0 - 10.0 m layer

[e] Main canopy cover = total percent canopy closure in the 10.0 - 20.0 m layer

[f] High canopy cover = total percent canopy closure > 20.0 m

[g] Total cover = b+c+d+e+f (maximum possible = 500 percent)

regression equation ($h = -0.21 + 0.50 f$, $r^2 = 0.88$, $P < 0.001$, $n = 29$) shows that doubling my edge densities to make them comparable to the full plot densities is a reasonable and conservative estimate. Patterns of bird density with increasing distance from the edge are shown in Figure 9 (pole-sapling/old growth) and Figure 10 (mature/old growth). A linear regression based on data pooled over years and all possible edge-interior contexts indicated density did not decrease with increasing distance from edge ($P = 0.33$). However using pooled data, density at the edge was greater than that in interior sites (Wilcoxon signed-ranks test, $P < 0.05$). This difference was also significant when data were pooled for both interior:edge combinations along the high contrast (pole-sapling/old growth) edge ($P < 0.05$) as well as the individual pole-sapling interior:edge (adjacent to old growth) ($P < 0.05$) and old growth interior:edge (adjacent to pole-sapling) ($P < 0.05$). Because of spatial limitations in the park my sample sizes are small and I cannot statistically compare densities between edge and interior sites along the low contrast mature/old growth edge. Inspection of Figure 10 indicates bird density is consistent with my hypothesis that bird density increased at the edge, but I have insufficient data to test this.

Using pooled data I conducted a linear regression between mean species richness (species encountered per half plot) and distance from edge. Species richness/half plot did not decrease with increasing distance from edge ($P = 0.47$). Patterns of mean species richness with distance from the edge are shown in Figure

11 (pole-sapling/old growth edge) and Figure 12 (mature/old growth edge). Using pooled data for all possible interior-edge contexts and between years, mean species richness was significantly greater at edges than in interior sites (Wilcoxon signed-ranks test $P < 0.05$). The relationship was also significant using only data from both interior-edge contexts along the high contrast (pole-sapling/old growth edge, Fig. 11) ($P < 0.05$) as well as for the individual old growth interior-edge (adjacent to pole-sapling stage) ($P < 0.05$) but not the individual pole-sapling interior-edge (adjacent to old growth stage) ($P > 0.05$). Because of spatial limitations in the park, my sample sizes are too small to statistically compare mean species richness between edge and interior plots along the low contrast (mature/old growth) edge. Inspection of Figure 12 suggests that species richness does not increase at low contrast edges.

Patterns of bird diversity/plot with increasing distance from edge are shown in Figure 13 (pole-sapling/old growth) and Figure 14 (mature/old growth). A linear regression using pooled data indicated that bird diversity/plot did not decrease with distance from the edge ($P = 0.25$). When data were examined for each context of edge, diversity/plot increased with distance from the edge at the old growth interior-edge (adjacent to mature stage (Fig. 14, $P = 0.05$). Bird diversity/plot at the edge was not different from that in interior plots (Wilcoxon signed-ranks test, $P > 0.05$).

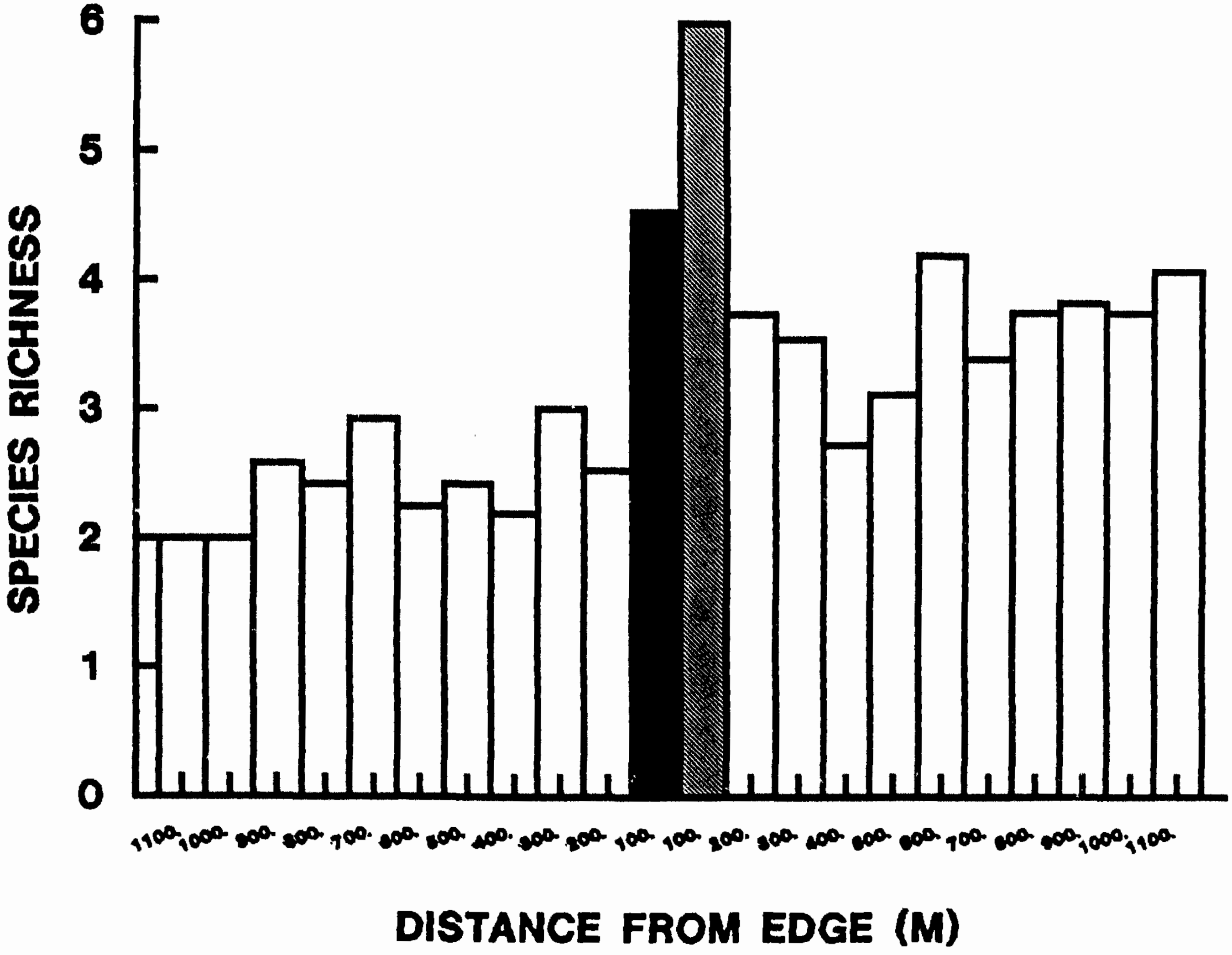

Figure 11. Mean species richness/half plot (number of species encountered/half plot) at different distances from the pole-sapling/old growth edge. Mean species richness in the edge half plots are shown in solid black (pole-sapling) and with cross hatching (old growth). White bars to the left of edge values represent mean species richness/half plot in pole-sapling interior. White bars to the right of edge values represent mean species richness/half plot in old growth interior.

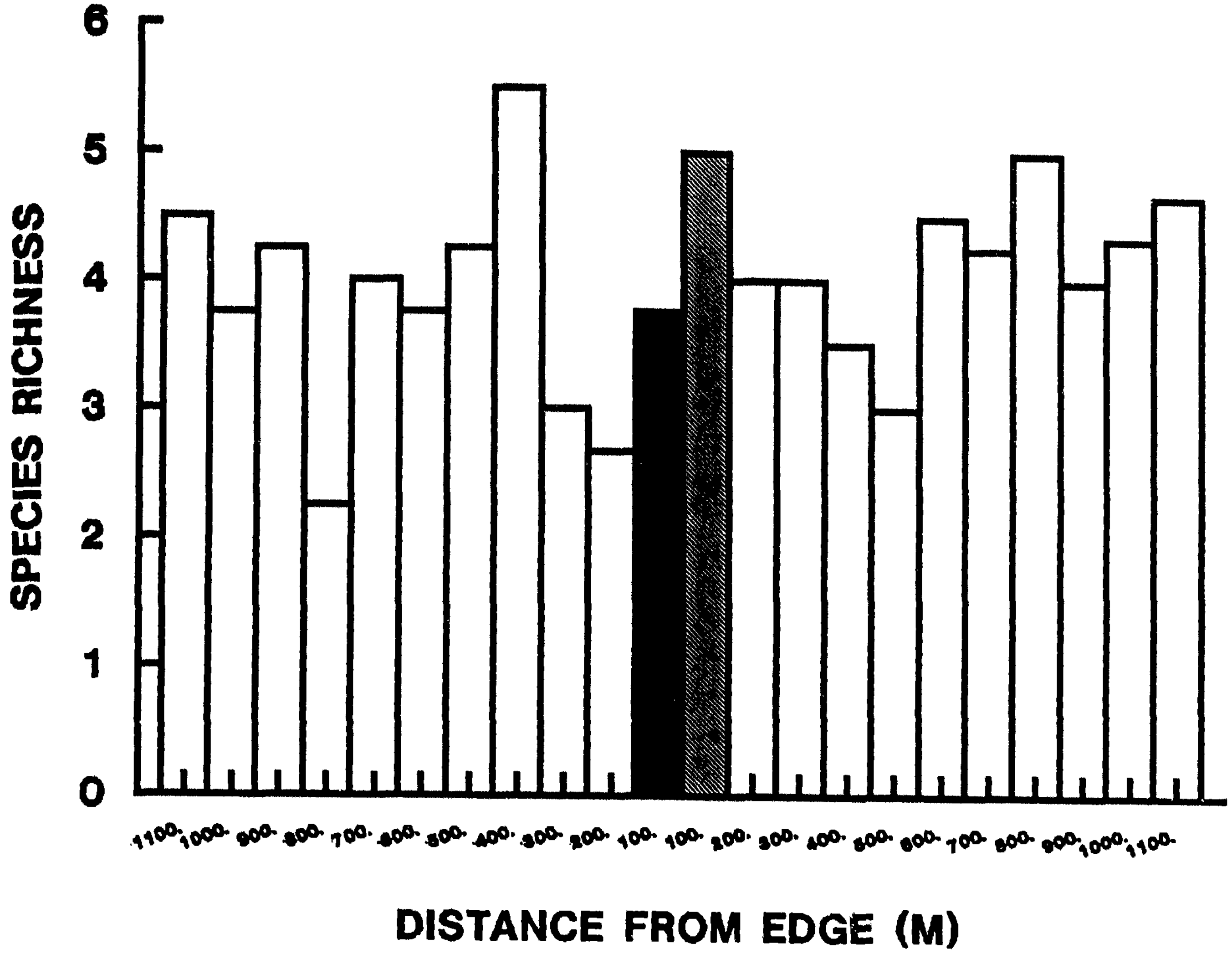

Figure 12. Mean species richness/half plot (number of species encountered/half plot) at different distances from the mature/old growth edge. Mean species richness in the edge half plots are shown in solid black (mature) and with cross hatching (old growth). White bars to the left of edge values represent mean species richness/half plot in mature interior. White bars to the right of edge values represent mean species richness/half plot in old growth interior.

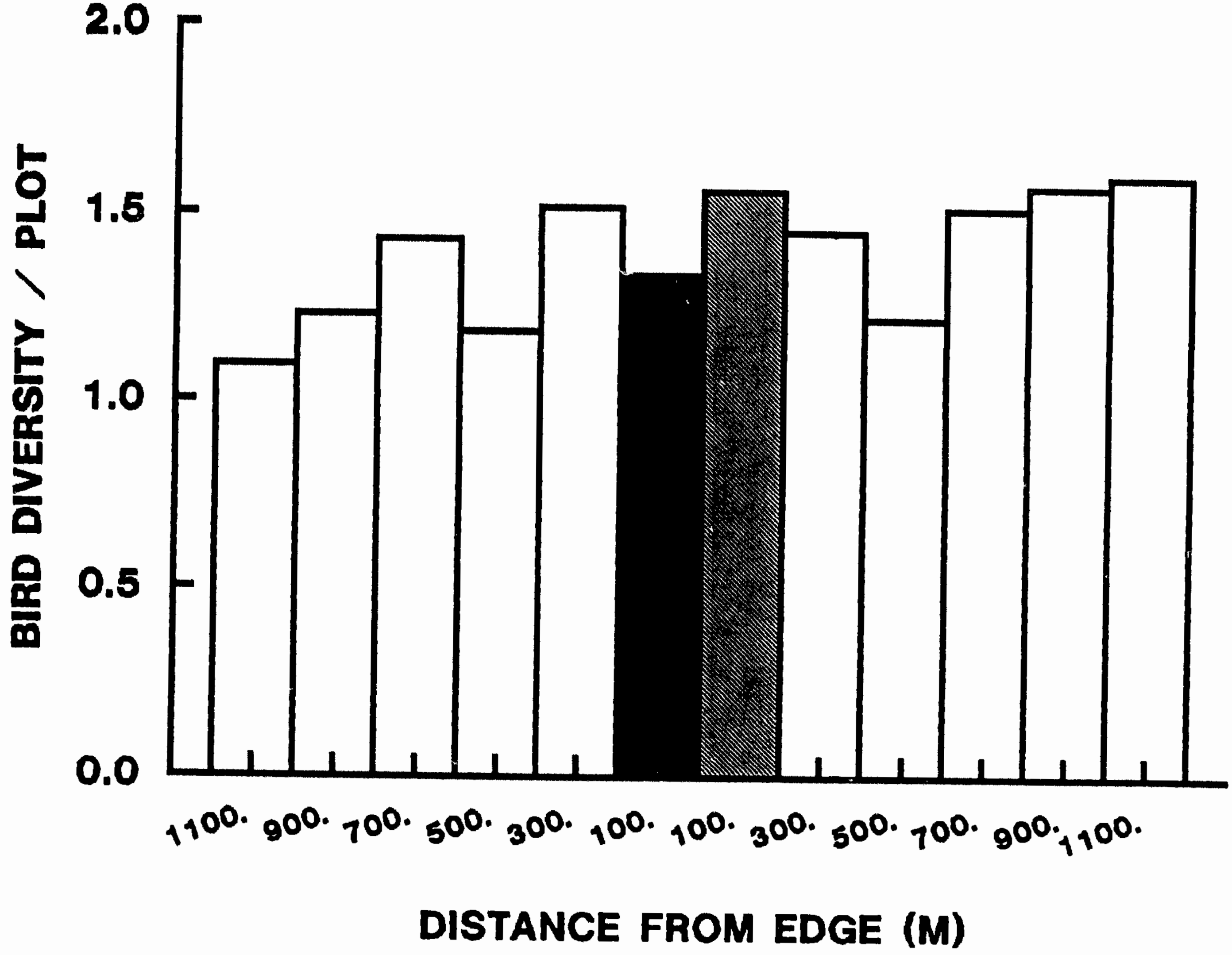

Figure 13. Mean bird diversity/plot (bird diversity/100 m radius plot) at different distances from the pole-sapling/old growth edge. Mean bird diversity/plot in the edge plots are shown in solid black (pole-sapling) and with cross hatching (old growth). White bars to the left of edge values represent mean bird diversity/plot in pole-sapling interior. White bars to the right of edge values represent mean bird diversity/plot in old growth interior.

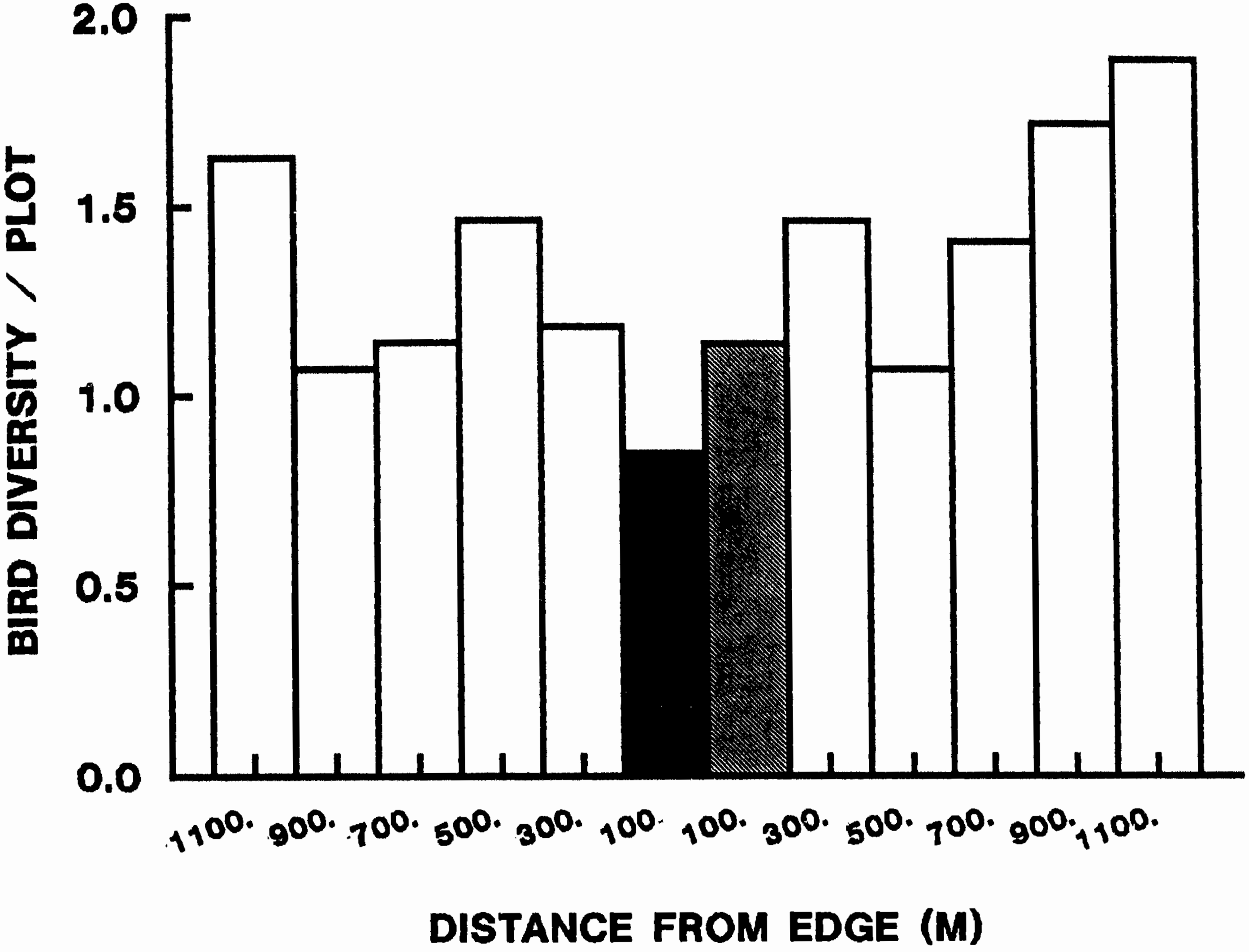

Figure 14. Mean bird diversity/plot (bird diversity/100 m radius plot) at different distances from the mature/old growth edge. Mean bird diversity/plot in the edge plots are shown in solid black (mature) and with cross hatching (old growth). White bars to the left of edge values represent mean bird diversity/plot in mature interior. White bars to the right of edge values represent mean bird diversity/plot in old growth interior.

DISCUSSION

The general pattern of increased bird densities and species richness at the edge compared with interior sites found in my study area are consistent with those of Strelke and Dickson (1980) and Hansson (1983). Hansson (1983) measured bird density along transects extending from forest edges 250 m out into clearcuts and the same distance inside forests. He found that density of many forest dwelling bird species is greater at the forest edge than further inside the forest, but he did not find this relationship for open habitat dwelling bird species. In my study area, both the individual old growth (adjacent to pole-sapling stage) and pole-sapling (adjacent to old growth stage) edges (Fig. 9) along the high contrast pole-sapling/old growth edge supported higher densities of birds than did homogeneous interior old growth and interior pole-sapling sites respectively. Whether or not an edge effect of increased density or species richness will be evident at an abrupt, induced edge compared with interior sites may be related to the numbers and densities of species present. There may be a threshold density or species richness, determined by the availability of habitat resources, below which no edge effect is apparent. Bird communities in clearcut habitats may be below this threshold while those in pole-sapling stages, and older, may have surpassed this threshold.

Considering only the high contrast pole-sapling/old growth edge, the edge effect of increased bird density at edge compared to interior habitats can be attributed to densities of only a few species. I define an "edge increaser" as a species whose density in edge habitats was consistently two times or more greater than that in interior habitats and an "edge avoider" as a species whose density in edge habitats was consistently less than half its density in interior habitats (Appendix 2). Edge increasers along the pole-sapling (adjacent to old growth stage) edge include Spruce Grouse, Rufous Hummingbird, Chipping Sparrow and Olive-sided Flycatcher while Dusky Flycatcher was an edge avoider. Edge increasers along the old growth (adjacent to pole-sapling stage) edge include Golden-crowned Kinglet, Swainson's Thrush and Wilson's Warbler while Winter Wren was an edge avoider. Whether a species is an edge increaser or an edge avoider appears to be habitat dependent. Townsend's Warbler also had much higher densities along the old growth (adjacent to pole-sapling) edge than in interior old growth.

Increased density and species richness at edges compared to interior habitats is not universal (Kroodsma 1982, Small and Hunter 1989). Small and Hunter (1989) examined the response of passerines to abrupt forest-river and forest powerline edges in Maine. They report that passerines showed no consistent edge effect: "richness and total density were not always greater near the edge than in the forest interior". Kroodsma (1982) also found that bird density was not greater at an abrupt powerline edge than in the forest interior. Small and Hunter (1989) suggested that the type of edge (inherent vs. induced) may determine whether or not an edge effect occurs. They draw their reasoning from Balda (1975) who suggested that permanent (inherent) edges may not support as diverse a bird species community as do temporary (induced) edges. Small and Hunter (1989) extended these ideas to density and suggested that perhaps density is also not enhanced in inherent edges. They point out that clearcut edges are always changing whereas the powerline edges were maintained every four years and the river edge was essentially permanent.

A number of explanations for the cause of edge effects have been proposed. Increased structural diversity of vegetation along an edge may provide life requisites that support greater densities and numbers of species than individual habitats on either side (Odum 1971). A richer insect fauna (Hansson 1983), higher primary productivity (Ranney et al. 1981), or greater light intensity (Strelke and Dickson 1980) may act alone, or in combination, to attract more birds to edge habitats. In my study area both the low and high contrast edges were relatively abrupt and thus no "ecotone" effect of greater structural diversity of vegetation was evident. Data on insect fauna, primary productivity, or light were not collected.

Creation of edge habitats traditionally has been viewed as "improvement" to existing habitats (Yahner 1988). However, Reese and Ratti (1988) point out that there may be fundamental faults with this paradigm. Excessive edge may lead to reduced populations of species dependent on large blocks of forest interior (Robbins 1979, Whitcomb et al. 1981). Reasons for this reduction may be due to a number of factors other than "area effects" of habitat fragmentation. Predators and brood parasites may be attracted to edge habitats (Bider 1968, Brittingham and Temple 1983). Wilcove (1985) found greater predation rates in smaller forest fragments (with more edge) than in larger forest blocks. Brood parasitism by Brown-headed Cowbird *(Molothrus ater)* has been implicated for reductions in a number of bird species in eastern deciduous forests (Mayfield 1965, Mayfield 1977, Brittingham and Temple 1983) and corvids have been implicated as the primary predators at edges (Wilcove 1985, Ratti and Reese 1988). Brown-headed Cowbirds were not observed in my study area and the only corvids present were Ravens and Gray Jays. Ravens were sighted flying over the study area but seldom seen amongst the vegetation. Gray Jays were never sighted within 100 m of a forest edge.

Rosenberg and Raphael (1986) studied the effects of habitat fragmentation of Douglas-fir forests on birds in California. The majority of species they considered showed no detrimental impacts from reduced forest patch size or from increased forest-clearcut edge. Rosenberg and Raphael (1986) suggested that the lack of negative aspects of edge creation in their study may be partially attributed to fragmentation and creation of induced edge in western coniferous forests that is "more recent and has not modified as great a proportion of the habitat as has occurred in the east". In addition, they point out that western montane forests may be naturally more diverse and have more inherent edge than do eastern deciduous forests because of the west's more rugged topography. As a result long term impacts of habitat modification, patch-size reduction and patch isolation may not yet be apparent and species of western coniferous forests may not experience the negative aspects of forest fragmentation as severely as do species in eastern deciduous forests.

The question of how edge contrast affects bird community characteristics as well as predation and brood parasitism rates is also important. For example, predation rates may be high in early successional stages and then decline as edge contrast declines, or vice versa depending on species and habitats (Reese and Ratti 1988). Although my sample sizes are small, inspection of relationships between edge contrast and bird community characteristics suggest that in the lower subalpine of Kootenay National Park, bird density, species richness and diversity decrease as edge contrast decreases.

Fires have had a significant effect on natural forest stands and succession both inside and outside of national parks. Thomas et al. (1978) remind us that burning, controlled or wild, creates induced edges and thereby increases habitat diversity of the forest. My study has shown that a corresponding change in the bird community will follow such a habitat alteration. Although negative aspects of edge creation have not yet been documented in western coniferous forests, data are limited and further research is needed.

CHAPTER 5

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Within coniferous forests, Harris (1984) suggested that three principal site characteristics influence the density and number of species occurring in a particular habitat: 1) elevation, 2) presence or absence of surface water and moistness of site, and 3) structural complexity of the vegetation, which is related to successional stage. In my study, all survey sites were approximately equidistant from surface water (e.g. creeks and rivers) and all were between 1500 and 1700 m elevation. What differed between successional stages was forest structure.

I found that bird community characteristics (density, species richness and species diversity) increased with successional age, although minor decreases occurred in young and old growth stages. These increases in bird density and diversity are related to the development of diverse vegetation structure which increases with successional age of the forest. Structural components of the vegetation (canopy height, percent cover of different vegetation layers, foliage volume and densities of snags and stumps) are related to bird community characteristics as well as the occurrence of feeding and nesting guilds of birds.

Forest edges influence bird communities in subalpine forests. Both the density and number of bird species were greater at edges than within the homogeneous interior of successional stages. Although not conclusive, my results also suggest that as edge contrast decreases, edge effects of increased density and species richness also decrease. In my study area, past forest fires have created a diverse habitat mosaic of successional stages. The structural differences of these successional stages in combination with the edges created due to their juxtaposition has resulted in a diverse bird community.

The National Parks Act and Canadian Parks Service policy (Parks Canada 1979) require that Western Region national parks protect both the vegetation landscape and the processes that contribute to the ecological character of that landscape. Although this policy suggests that under ideal circumstances fire will be allowed to run its course, conditions are rarely ideal so the policy further recognizes that active management may be necessary.

The aim of fire management in Western Region national parks is to preserve natural heritage resources and protect all other values through a deliberately planned fire control and fire use programme that is ecologically sound and cost effective. A major goal of fire management is to allow fire to achieve its natural role within park ecosystems with the objectives of: 1) perpetuating naturally occurring plant and animal species, 2) perpetuating naturally occurring vegetation patterns and mosaics and 3) maintaining a natural fire regime. Controlled use of fire has recently been implemented in Banff National Park and is being considered in other Western Region national parks. Recent fire history studies in Kootenay (Masters 1989), Banff (White 1985) and Jasper National Parks (Tande 1979), all show that the age class distribution of forests is skewed to older ages indicating a lack of disturbance in recent decades. White (1985) suggests that fire prevention and suppression is responsible for the skewed age class distributions. Because of the difficulties in maintaining a natural age-class distribution based only on random (by lightning or unplanned man-caused) patterns of ignition, the Canadian Parks Service has begun to use prescribed fire to create the mosaics called for in vegetation management plans (Hawkes 1990). This may be the best approach as a future forest mosaic by design may be better than that which we might inherit by default.

Fires have had a significant effect on natural forest stands and succession both inside and outside of National Parks. Forest fires, controlled or wild, increase structural diversity in a forest and in response bird communities change to include those species best adapted to, and most favored by, the new habitat complex.

Maser and Thomas (1978) expressed the need to shift our focus from management for the present to management for the future. They suggested that this can only be accomplished through an ability to predict outcomes of planned events. Successional stages following fire are recognizable and because succession is a sequential process the stages are also predictable (Edgerton and Thomas 1978). My study has shown that fire induced secondary succession in subalpine forest systems is accompanied by corresponding changes in the bird community. There were differences in bird communities between early successional and late successional stages and a number of species appear to rely on fire to create favorable habitats. The birds which occur naturally in different successional stages are not random assemblages, but represent species which occur together because of common adaptations to one another, to their food and to habitat resources. Fire is an important natural process in National Park ecosystems which must be allowed to occur if objectives of perpetuating naturally occurring vegetation patterns and naturally occurring plant and animal communities are to be met.

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Appendix 1. Acronyms, common names, scientific names, foraging guilds and nesting guilds for birds mentioned in the text. Bird names follow AOU (1983).

	Species	Scientific Name	Foraging Guild[a]	Nesting Guild[b]
SPGR	Spruce Grouse	*(Dendragapus canadensis)*	GRFO	GRND
HAOW	Northern Hawk-Owl	*(Surnia ulula)*	PRED	CAVI
BLSW	Black Swift	*(Cypseloides niger)*	SALL	CLIF
RUHU	Rufous Hummingbird	*(Selasphorus rufus)*	NECT	SHRB
HAWO	Hairy Woodpecker	*(Picoides villosus)*	DRIL	CAVI
NOWO	Three-toed Woodpecker	*(Picoides tridactylus)*	DRIL	CAVI
COFL	Northern Flicker	*(Colaptes auratus)*	GRGL	CAVI
PIWO	Pileated Woodpecker	*(Dryocopus pileatus)*	DRIL	CAVI
OLFL	Olive-sided Flycatcher	*(Contopus borealis)*	SALL	TREE
WEPE	Western Wood Pewee	*(Contopus sordidulus)*	SALL	TREE
HAFL	Hammond's Flycatcher	*(Empidonax hammondii)*	SALL	TREE
DUFL	Dusky Flycatcher	*(Empidonax oberholseri)*	SALL	SHRB
GRJA	Gray Jay	*(Perisoreus canadensis)*	CAFO	TREE
CLNU	Clark's Nutcracker	*(Nucifraga columbiana)*	CAFO	TREE
CORA	Common Raven	*(Corvus corax)*	GRSC	CLIF
BCCH	Black-capped Chickadee	*(Parus atricapillus)*	CAGL	CAVI
MOCH	Mountain Chickadee	*(Parus gambeli)*	CAGL	CAVI
BOCH	Boreal Chickadee	*(Parus hudsonicus)*	CAGL	CAVI
RENU	Red-breasted Nuthatch	*(Sitta canadensis)*	BAGL	CAVI
BRCR	Brown Creeper	*(Certhia americana)*	BAGL	CAVI
WIWR	Winter Wren	*(Troglodytes troglodytes)*	GRGL	GRND
GOKI	Golden-crowned Kinglet	*(Regulus satrapa)*	CAGL	TREE
RUKI	Ruby-crowned Kinglet	*(Regulus calendula)*	CAGL	TREE
TOSO	Townsend's Solitaire	*(Myadestes townsendi)*	SALL	GRND
SWTH	Swainson's Thrush	*(Catharus ustulatus)*	GRFO	SHRB
HETH	Hermit Thrush	*(Catharus guttatus)*	GRGL	GRND
ROBI	American Robin	*(Turdus migratorius)*	GRFO	TREE
VATH	Varied Thrush	*(Ixoreus naevius)*	GRGL	TREE
BOWA	Bohemian Waxwing	*(Bombycilla garrulus)*	SALL	TREE
TEWA	Tennessee Warbler	*(Vermivora peregrina)*	CAGL	GRND
ORWA	Orange-crowned Warbler	*(Vermivora celata)*	CAGL	GRND
YRWA	Yellow-rumped Warbler	*(Dendroica coronata)*	CAGL	TREE
TOWA	Townsend's Warbler	*(Dendroica townsendi)*	CAGL	TREE
MCWA	MacGillivray's Warbler	*(Oporornis tolmiei)*	CAGL	TREE
WIWA	Wilson's Warbler	*(Wilsonia pusilla)*	CAGL	GRND
CHSP	Chipping Sparrow	*(Spizella passerina)*	GRFO	TREE
FOSP	Fox Sparrow	*(Passerella iliaca)*	GRFO	GRND
LISP	Lincoln's Sparrow	*(Melospiza lincolnii)*	GRFO	GRND
DAJU	Dark-eyed Junco	*(Junco hyemalis)*	GRFO	GRND
WHCR	White-winged Crossbill	*(Loxia leucoptera)*	CAFO	TREE
PISI	Pine Siskin	*(Carduelis pinus)*	CAFO	TREE
EVGR	Evening Grosbeak	*(Coccothraustes vespertinus)*	CAFO	TREE

[a] BAGL = bark gleaner, CAGL = canopy gleaner, CAFO = canopy forager, GRFO = ground forager, GRGL = ground gleaner, PRED = predator, SALL = air sallyer, NECT = nectar feeder, GRSC = ground scavenger

[b] typical nest locations are TREE = tree, GRND = ground, SHRB = shrub, CAVI = tree cavity, CLIF = cliff

Appendix 2. Mean densities (individuals/40 ha ± SE) of birds encountered in edge and interior habitats along the high contrast pole-sapling/old growth edge in lower subalpine forests of Kootenay and Banff National Parks, during the breeding season, 1989-90.

	Pole-sapling				Old growth			
	1989		1990		1989		1990	
Species Code[a]	Interior (10)[b]	Edge (2)	Interior (6)	Edge (2)	Interior (10)	Edge (2)	Interior (6)	Edge (2)
SPGR	3.2± 1.4	8.5± 0.0	4.2± 1.3	22.1±11.9	6.7± 2.5	12.7± 4.2	4.2± 2.1	4.2± 4.2
RUHU	-[c]	12.7±12.7	1.1± 1.1	16.1± 0.8	0.4± 0.4	10.6± 2.1	-	4.2± 4.2
NOFL	1.6± 1.1	4.2± 0.0	2.1± 1.3	2.1± 2.1	1.3± 0.8	-	1.1± 1.1	-
OLFL	2.1± 1.1	25.5± 8.5	5.3± 3.0	33.5±12.3	4.5± 1.2	17.0± 8.5	1.6± 1.6	-
DUFL	3.2± 1.4	-	13.8± 2.6	4.2± 4.2	-	-	-	-
GRJA	-	-	-	-	0.6± 0.6	-	1.1± 1.1	-
CLNU	2.0± 1.0	4.2± 4.2	0.5± 0.5	-	0.7± 0.5	-	-	9.3± 0.8
BCCH	-	-	-	-	3.4± 1.5	21.2±21.2	-	-
MOCH	1.3± 0.8	-	-	-	0.8± 0.8	-	-	-
BOCH	-	-	-	-	0.6± 0.6	-	4.2± 4.2	10.2± 0.8
RENU	0.6± 0.6	-	1.6± 1.1	4.2± 4.2	2.8± 1.0	-	9.5± 4.2	37.3± 3.4
WIWR	-	-	-	-	6.8± 2.8	-	14.9± 3.1	-
GOKI	-	-	-	-	10.2± 4.5	25.5±25.5	30.8± 7.4	78.7±11.9
RUKI	-	-	-	-	0.8± 0.8	-	-	-
TOSO	4.2± 2.5	-	-	-	-	-	-	-
SWTH	11.2± 2.7	14.9± 2.1	29.2± 3.8	19.9± 9.8	13.7± 3.0	40.4±19.1	20.7± 5.6	47.5±11.9
HETH	12.1± 2.3	17.0± 0.0	9.6± 2.7	5.1± 5.1	1.3± 1.3	17.0±17.0	2.7± 5.6	-
ROBI	3.2± 1.5	10.6± 2.1	8.0± 3.0	15.3±15.3	5.5± 1.8	8.5± 0.0	2.1± 2.1	-
VATH	-	-	-	-	1.3± 0.9	-	6.4± 2.3	5.1± 5.1
BOWA	2.0± 1.1	-	0.5± 0.5	-	0.7± 0.5	-	2.7± 1.3	2.1± 2.1
ORWA	-	-	-	-	0.6± 0.6	-	-	-
YRWA	8.0± 1.8	8.5± 8.5	13.8± 3.9	40.7±10.2	4.9± 2.3	6.4± 2.1	13.8± 5.6	25.5±25.5
TOWA	-	-	-	4.2± 4.2	61.8± 7.2	101.9± 0.0	81.7± 7.1	111.1± 8.5
MCWA	-	-	2.1± 2.1	28.0± 2.5	-	-	-	8.5± 8.5
WIWA	16.6± 4.1	25.5± 0.0	29.2± 7.9	28.9±11.9	13.0± 2.7	27.6± 6.4	4.2± 2.1	49.2±18.7
CHSP	-	8.5± 8.5	-	8.5± 8.5	3.0± 1.2	-	4.2± 3.1	4.2± 4.2
FOSP	-	-	-	-	-	-	4.2± 2.7	-
DAJU	21.2± 2.6	42.4± 8.5	20.7± 4.0	37.3± 3.4	18.5± 3.1	12.7± 8.5	13.8± 3.9	36.5± 5.9

[a] see Appendix 1 for species codes (mnemonics)
[b] "()" number of circular bird plots
[c] "-" not encountered

Appendix 3. Pearson correlation coefficients for 14 variables characterizing the structure and composition of vegetation in five successional stages of the Lower Subalpine in Kootenay and Banff National Parks, 1989-90.

	Vegetation Variables												
	CHGT	HCOV	LSCOV	HSCOV	MCLO	HCLO	TCOV	TVOL	SNAGS	SNAGD	SNAGP	SNAG	FHD
HCOV	-0.07												
LSCOV	0.12*[a]	0.61*											
HSCOV	0.51*	0.16*	0.43*										
MCLO	0.25*	-0.28*	-0.12*	0.06									
HCLO	0.50*	-0.10	0.01	0.60*	-0.18*								
TCOV	0.51*	0.49*	0.65*	0.84*	0.12*	0.59*							
TVOL	0.54*	-0.10	0.05	0.68*	0.36*	0.59*	0.62*						
SNAGS	-0.25	0.23*	-0.09	-0.08	-0.25*	0.02	-0.03	-0.14					
SNAGD	0.14	0.10	0.14	0.16*	-0.17	0.09	0.12	0.07	0.07				
SNAGP	0.00	-0.14	-0.01	-0.03	0.35*	-0.07	0.01	0.03	-0.17*	-0.15			
SNAG	-0.02	0.16*	-0.00	0.00	-0.13	0.02	0.04	-0.06	0.77*	0.48*	0.27*		
FHD	0.75*	0.05	0.38*	0.66*	0.27*	0.53*	0.71*	0.57*	-0.21*	0.14	0.11	-0.05	
TSD	0.42*	-0.12*	-0.05	0.26*	0.15*	0.31*	0.24*	0.26*	-0.08	0.00	-0.00	-0.07	0.37*

[a] * significant, $P < 0.05$