EFFECTS OF CLEARCUTTING ON LANDSCAPE STRUCTURE AND BIRD SPECIES DIVERSITY AND ABUNDANCE IN THE ROCKY MOUNTAINS

by

PIERRE RAOUL PAUL VERNIER

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Department of FOREST SCIENCES

The University of British Columbia
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Abstract

Even-aged, short-rotation forest practices are increasingly replacing wildfires as the dominant large-scale disturbance process in many forest landscapes of British Columbia. The resulting landscape patterns are often dramatically different from historical patterns with consequences for forest birds and other wildlife species that are poorly understood, especially at the landscape level. The goal of this study was to assess the effects of clearcutting on the structure of forest landscapes and to describe the response of birds to these structural patterns. The study was conducted in the managed and protected landscapes within the montane spruce biogeoclimatic zone on the western slopes of the Rocky Mountains.

Forest cover maps, biophysical habitat maps, aerial photographs, and a geographic information system were used to create a habitat patch map of the montane spruce zone. The effects of clearcutting on landscape structure were assessed by comparing current managed landscape patterns to patterns in adjacent protected areas and to historical conditions within the same landscape. Landscapes were quantified using a variety of indices measuring compositional and configurational aspects of spatial structure. The results of a bird survey undertaken in 117 plots located in the same area were then overlaid on the habitat patch map to describe bird responses to current landscape conditions. Multiple regression analysis was used to model the relations between birds and surrounding habitat patterns measured in concentric circles ranging in area from 0.8 ha to 314.2 ha.

The spatio-temporal analysis of landscape patterns revealed several differences between 'managed' and 'unmanaged' forest landscapes which can be attributed to clearcutting. In particular, clearcutting has (1) increased the number of early-, mid-, and late-seral forest patches, (2) increased the total area of early-seral habitat at the expense of late-seral forest habitat and to a lesser extent of mid-seral forest habitat, (3) reduced the total area of mature interior forest habitat while increasing the number of core areas, (4) increased the total area of mature forest edge habitat, (5) increased the density of high contrast edges, (6) reduced mean patch size and variability of mid- and late-seral forest patches, (7) simplified the overall shape of patches in the landscape while increasing the complexity of late-seral forest patches, (8) increased patch diversity, and (9) reduced patch contagion.

Bird responses to surrounding habitat patterns varied with respect to the strength and nature of the relationships. Landscape variables explained between 43% and 51% of the variation in bird species richness, diversity, and total abundance. Mature forest edge habitat was the strongest predictor variable in each case. Landscape variables explained between 25% and 49% of the variation in the abundance of 10 bird species analysed. One group of birds (Chipping Sparrow, Dark-eyed Junco, Vesper's Sparrow, and Orange-crowned Warbler) was associated with the proportion of clearcuts in the surrounding landscape. Another group (Red-breasted Nuthatch, Golden-crowned Kinglet, Townsend's Sparrow, Brown Creeper, and Swainson's Thrush) was associated with the proportion of mature forest edge and interior habitat. One species, Yellow-rumped Warbler, was best predicted by the amount of young forest and edge habitat. The strengths of the relationships were greatest for the 12.6 ha and 19.6 ha concentric circles.

Many more observational studies of this type, repeated in different locations, will be necessary to improve our understanding of the interactions among landscape patterns, natural disturbance processes, and human activities. Moreover, a more profound understanding of the influence of landscape structure on birds will depend on more analytical investigations which rely on better quality landscape-level habitat data collected for that purpose.

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1.0 Introduction

1.1 Introduction

Forest practices in British Columbia and western North America are changing the composition and spatial arrangement of habitat patches in forest landscapes with consequences for wildlife species that are poorly understood (Hansen *et al.* 1991, Rolstad 1991). Many landscapes that were once dominated by an extensive and contiguous matrix of late-seral forests are rapidly being converted to heterogeneous mosaics of early-, mid-, and late-seral forest patches with a high density of human-induced forest edges (Hunter 1990). In addition to late-seral habitat loss and fragmentation, forest practices are also creating new disturbance types and altering natural disturbance regimes (Turner 1989). The response of forest birds and other wildlife species to these managed landscape patterns is currently the topic of much research in the resource management sciences (Ruggiero *et al.* 1991, Hansson 1992).

Research on the effects of forest practices on habitat and wildlife is generally considered at two broad spatial scales, the stand or within-patch level and, more recently, the landscape level (Hansen *et al.* 1993). At the stand level, forest practices have changed within-patch structure by eliminating large live trees and snags, reducing coarse woody debris, excluding competing shrubs and deciduous trees, reducing tree, shrub, and herb species diversity, reducing horizontal patchiness due to canopy gaps, converting multi-aged, multi-layered stands into even-aged, single layer stands, and reducing or eliminating other structural elements (Norse 1990, Bunnell *et al.* 1991). At the landscape level, forest practices have changed structure by converting late-seral forests to modified early- and mid-seral forests, reducing the time and space occupied by natural early- and late-seral forests, isolating remnant late-seral forest patches, increasing the density of high-contrast edges (i.e., boundaries between mature forests and clearcuts or natural openings), decreasing the mean size of patches, simplifying the shapes of patches, increasing the proportion of edge habitat, decreasing the connectivity of mature forest interior habitat (i.e., the core area within a patch or matrix beyond some specified edge distance or buffer width), increasing patch diversity, and altering the spatial arrangement of patches (Li and Reynolds 1993, Rogers 1993).

The diversity and abundance of bird species appear to be influenced by habitat characteristics at several spatial scales including the stand and landscape levels (Hutto 1985, Krebs 1994). Bird responses at the stand level are related to the internal composition and structure of habitat patches (Dunning *et al.* 1992). For example, patches that are characterized by abundant resources, multiple vertical layers, and horizontal patchiness are often positively correlated with species richness and abundance (Hunter 1990). Although the relation to within-habitat factors is relatively well understood, it is becoming clear that birds are also influenced by landscape factors such as patch diversity, size, shape, and isolation (Rolstad 1991). Landscape factors are interrelated, though, and their effects on birds are difficult to separate. For example, core habitat is related to patch size, shape, adjacency, and isolation. Moreover, landscape level effects are related to the scale at which each species uses habitat and the scale of the heterogeneity of the surrounding landscape.

The number and proportion of habitat patch types in a landscape may determine the pool of potential species that occur in a given landscape (Wiens 1989b). For example, the regional distribution of forest stands of different age classes influenced the distribution of forest birds in the boreal forests of Finland (Haila 1991). In general, heterogeneous landscapes containing a variety of patch types in different age classes contain more species than a homogeneous landscape containing a few large, contiguous patches (Hunter 1990). At a more local scale, bird populations and communities appear to be influenced by surrounding habitat patterns. The number and proportion of surrounding habitat types, for instance, were found to be important predictors of bird species diversity and abundance by Pearson (1993).

Patch size and shape, which directly affect the distribution and relative proportion of mature forest edge and interior habitat, may also influence bird species diversity and abundance. Species diversity in large patches is generally higher than in smaller patches (McIntyre 1995). Patch size may also be the best predictor of population density for forest-dependent species (Rolstad 1991). In highly fragmented landscapes, however, some species with large area requirements, such as Barred Owls (*Strix varia*), may be able to increase the effective size of their territory by foraging in a number of smaller patches within their dispersal capability (Dunning *et al.* 1992). The shape of a patch can moderate the effect of patch size. For example, large patches with high edge-to-area ratios (i.e., corridors) may not be suitable for species associated with late successional forest interior conditions.

Bird species may also be affected by patch boundary characteristics (Wilcove 1985, Catt 1991). Edge effects, the ecological changes that occur at the boundaries of ecosystems (i.e., changes in light, wind, humidity, and species composition), can adversely affect forest interior species both locally and regionally. Brood predation and nest parasitism are examples of edge effects which occur at a local scale but can influence the distribution and abundance of forest interior species at the landscape level (Whitcomb *et al.* 1981, Angelstam 1991). Managed landscapes with a high density of forest-to-clearcut edges may have more bird species than natural landscapes due to increases in generalist and edge species (Hunter 1990). These same landscapes, though, may contain far fewer forest interior species and/or edge-sensitive bird species (Temple 1991).

Patch isolation may also influence habitat use, especially for bird species with limited dispersal capabilities (Rolstad 1991). For example, a forest which is fragmented into isolated patches may contain fewer species than a forest with well connected patches (Blake and Karr 1987). Small, isolated patches may also provide poor conditions for forest interior species (Harris 1984, Temple 1985). In some cases, the combination of several factors may determine the suitability of a patch or landscape. Habitat use by the Northern Spotted Owl (*Strix occidentalis caurina*), for instance, appears to be influenced by several landscape factors including habitat type, isolation, and patch size variability (Lemkhul and Raphael 1993).

Forest management is evolving from the sustained yield of individual resources such as tree and deer species to the conservation and sustainable management of all native species, ecosystems, and ecological processes (CSP 1995, Galindo-Leal and Bunnell 1995). Under these new perspectives it is of paramount importance to better understand the conditions necessary to maintain a full complement of bird species and habitats in managed forest landscapes. The present study intends to contribute to this understanding by using geographic information systems (GIS), forest cover maps, and bird abundance data within a landscape approach.

1.2 Objectives

The goal of this study was to assess the effects of logging on the structure of forest landscapes in the Rocky Mountains and to describe the response of birds to these structural patterns. A study area comprising managed and protected forests within the montane spruce biogeoclimatic zone was selected to assess the spatial and temporal effects of clearcut logging on landscape structure. In addition, the results of a bird survey undertaken in the same area was used to describe bird responses to current landscape conditions. The specific objectives were:

1. to compare the composition and configuration of habitat patches in the managed and protected montane spruce forest landscapes in 1993;
2. to describe temporal changes in the composition and configuration of early, mid, and late-seral forest patches in the managed montane spruce landscape between 1953 and 1993; and

3. to analyse the relations between bird species diversity and abundance and surrounding habitat patterns.

1.3 Forest Landscape Concepts and Terminology

The characterization of landscape structure is an important prerequisite to better understanding and managing forest landscapes as ecological systems. A landscape is "a heterogeneous land area composed of an interacting mosaic of patches, at any scale, relevant to the phenomenon (e.g., species) under consideration" (McGarigal and McComb 1995). The size and shape of a landscape can be defined by ecological boundaries (e.g., watersheds or biogeoclimatic zones), arbitrary boundaries (e.g., land use or management zones) or a combination of both. In wildlife-habitat studies, patches or habitat patches are defined in terms of habitat attributes that are important to a species or a community (Lemkhul *et al.* 1991, Pearson 1993, McGarigal and McComb 1995). A forest patch is a contiguous area of land that is relatively homogeneous with respect to forest type, seral stage, and canopy closure (Forman and Godron 1986). An example would be a young lodgepole pine forest patch. A non-forest patch is a contiguous area of land or water that is homogeneous with respect to broad vegetation types, such as a wetland.

Forest and non-forest habitat occur as patches, corridors and matrix (Forman and Godron 1986). The matrix is the most contiguous and extensive patch type in the landscape and dominates landscape functioning and dynamics. In the Pacific Northwest, the matrix often comprises late successional and old growth forests. Corridors are linear habitats (e.g., riparian corridors) which connect or functionally integrate two or more patches. Patches, especially late-seral forest patches, are sometimes characterized as being composed of interior and edge habitat. Interior or core habitat refers to the portion of a patch (or matrix) which is essentially unaffected by neighbouring patches; this is the interior region of the patch. Edge habitat refers to a band on the periphery of a patch or matrix that differs with respect to light, wind, humidity and species composition from the core.

The effects of spatial and temporal scales are of primary importance in landscape analyses (Turner 1989). Different patterns emerge at different scales of investigation (Wiens 1989a). Scale in categorical maps has several components including grain and spatial extent. Grain and extent can be defined from a statistical or an organismic point of view (McGarigal and Marks 1993). From a statistical perspective, grain is the size of the individual sampling unit. In many GIS studies, grain is equivalent to pixel size or minimum mapping unit and is limited by the scale of existing maps or satellite imagery. Grain defines the lower limit of resolution beyond which landscape patterns cannot be detected. Spatial extent refers to the geographical region which encompasses the sampled units (i.e., the study area). Spatial extent defines the upper limit of resolution. Together, grain and extent form the statistical spatial bounds of a landscape ecological study.

In contrast, from an organism's perspective, grain and extent are dependent on the species of concern. Grain is the minimum unit of space that an organism can differentiate. Extent may be defined by home range size at the organism level, region or landscape at the population level, and geographic distribution at the species level (McGarigal and Marks 1993). Moreover, animals probably respond to landscape heterogeneity at several scales (i.e., choosing between food items and choosing between foraging sites). Ideally, the statistical and organismic definitions of scale for a particular study should be similar and should depend on the species and process of interest. The context of a patch or landscape may also be of critical importance to wildlife species. Patches and landscapes are connected to other patches and landscapes by the movement of organisms within an ecological region (Forman and Godron 1986). Many vagile species with large home ranges such as songbirds may use different patches and landscape types to meet breeding and feeding requirements (Wiens 1989b).

Characterizing landscape structure generally amounts to quantifying the geometry, composition, and spatial arrangement of patches in categorical vegetation or forest cover maps (Figure 1) (Li and Reynolds 1993). Many indices have been proposed to characterize the various aspects of landscape structure (Forman and Godron 1986, O'Neill *et al.* 1988, Turner 1989), and more are continuously being proposed (Li and Reynolds 1993, Olsen *et al.* 1993, Loehle and Wein 1994). Most of these indices have been described in detail in several recent reviews (McGarigal and Marks 1993, Rogers 1993, Baskent 1995).

Indices of landscape geometry measure the physical dimensions (usually size and shape) of an individual patch, a patch type, or the landscape as a whole (Rogers 1993). Indices of landscape composition measure the number, the proportion, and the diversity of patch types. Indices of landscape configuration measure the spatial arrangement of patches, the contrast between neighbouring patches, and the connectivity of patches of the same type. Indices that quantify the amount and density of forest edges measure landscape composition but they can also be used as a basis for calculating configuration metrics such as nearest-neighbour indices.

Some indices, such as the proportion and distribution of seral stages, can be interpreted as indicators of disturbance processes (Noss 1990). Many of the patch-type level metrics can be interpreted as measures of habitat fragmentation while landscape level metrics can be interpreted as measures of landscape heterogeneity (McGarigal and Marks 1993). Finally, core habitat metrics can also be calculated in the same way as patch and patch type metrics to provide information on the number, proportion, connectivity, and spatial arrangement of forest interior habitat patches.

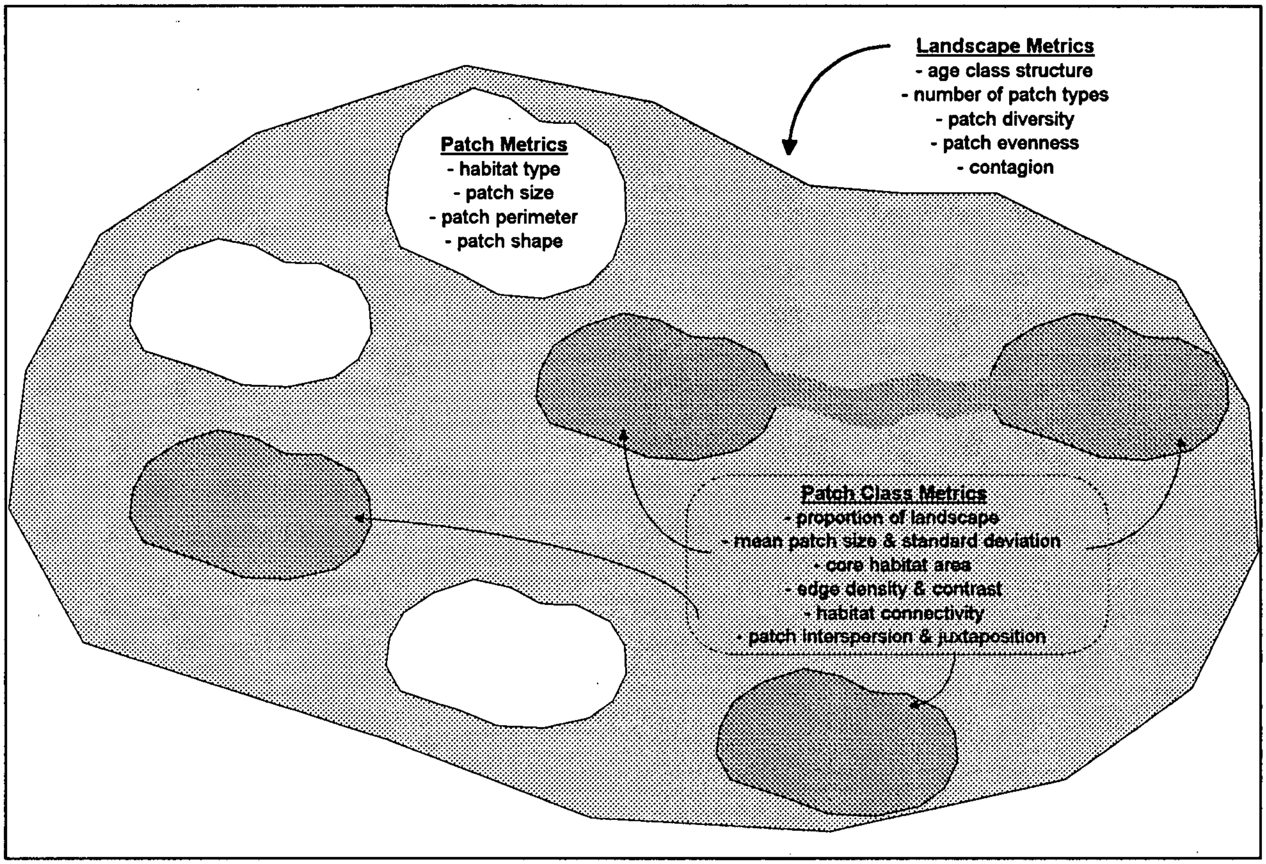


Figure 1: Common patch, patch type, and landscape metrics used to characterize forest landscape structure.

2.0 Study Area

The Beaverfoot study area is located in and adjacent to Kootenay and Yoho National Parks along the western slopes of the Rocky Mountains of British Columbia, extending from about 50.8° to 51.2° North Latitude and 116.0° to 116.4° West Longitude (Figure 2). The total area is 66,239 ha. Although referred to as the 'Beaverfoot', the study area actually comprises portions of two contiguous watersheds: the Beaverfoot and the Kootenay. Like many of the valleys in the Rocky Mountains, the Beaverfoot and Kootenay watersheds are oriented in a southeast to northwest direction. The Beaverfoot watershed lies to the northwest of the Kootenay watershed. The Beaverfoot and Kootenay valleys are relatively wide and thus contain more lower elevation montane forests (1000 - 1800 metres) than many other valleys in the western side of the Rocky Mountains. Many of these forests lie in the managed area which connects the two National Parks. The lower elevation forests may be important as travel corridors and winter range for many species (Achuff *et al.* 1984). The majority of the study area, though, is being actively managed for timber with undetermined consequences for the region's wildlife.

The Beaverfoot spans four biogeoclimatic zones: interior cedar-hemlock (ICH), montane spruce (MS), Engelmann spruce - subalpine fir (ESSF), and alpine tundra (AT). The MS zone (20,093 ha), the focus of this study, is common at lower elevations (1100-1650 metres). Zonal climax trees include Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*). The dominant subzone is the dry cool MS subzone (MSdk) which is characterized by extensive stands of seral lodgepole pine (*Pinus contorta*) due to frequent forest fires in the past.

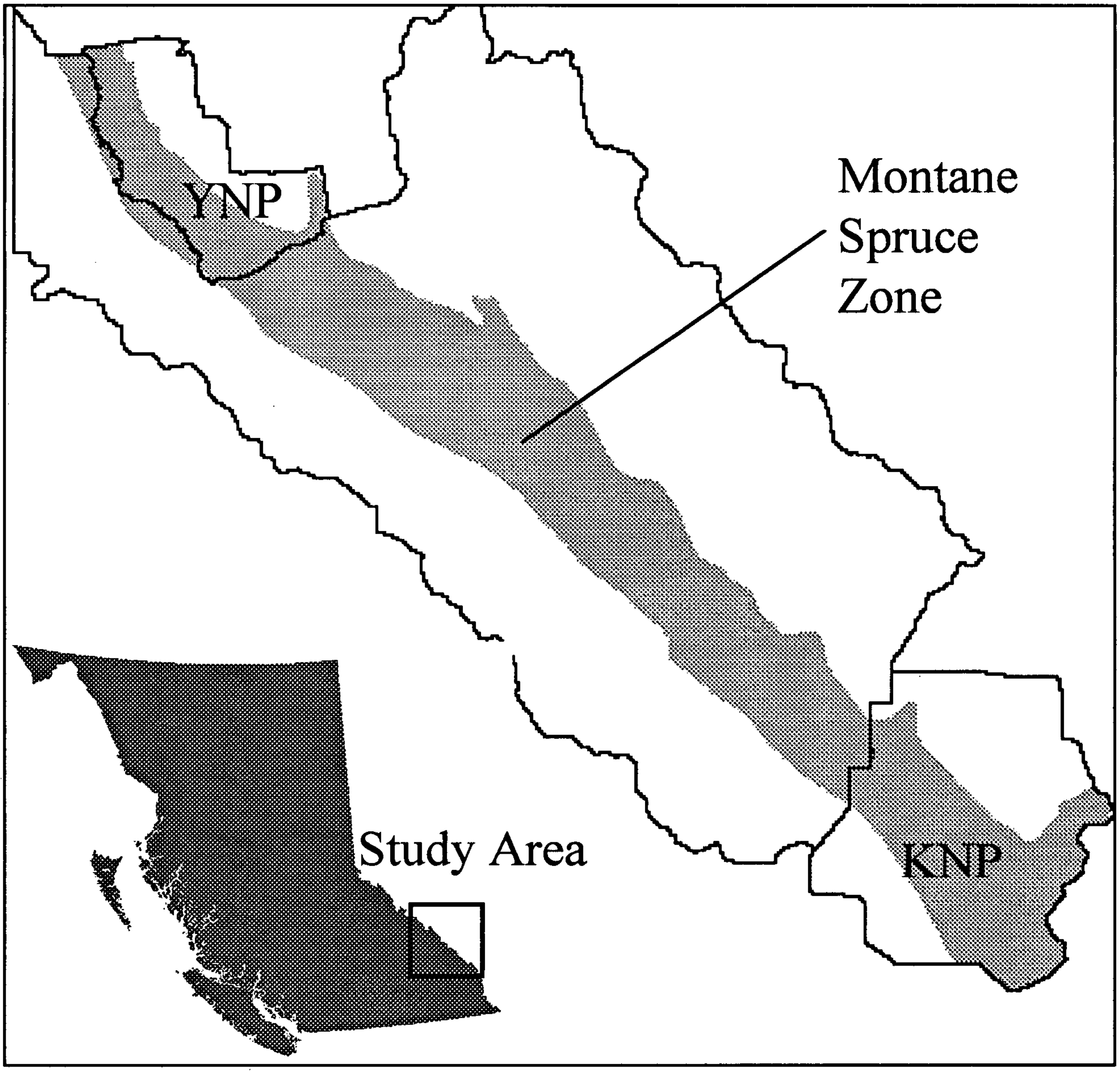


Figure 2: The managed and protected montane spruce forest landscapes of the Beaverfoot study area located on the western slopes of the Rocky Mountain, British Columbia. KNP = Kootenay National Park; YNP = Yoho National Park.

Historically, stand replacing (crown) fires have been the dominant disturbance process shaping the forested landscapes until the beginning of this century (Masters 1989). Fire suppression has since been practiced in both the managed and protected landscapes. Since the middle of the century, the managed forests of the Beaverfoot have been logged extensively, removing approximately 40% of the forest. Most of the logging has taken place in the lower elevations resulting in a distinct pattern of regularly spaced clearcuts of varying sizes embedded in a late successional forest matrix. The density of logging roads is high at the lower elevations, tapering off with altitude. Very little contiguous mature forest habitat remains in the MS, ICH, and lower elevation ESSF zones in the managed area.

In contrast to the managed landscape patterns, fire management practices in the protected areas have effectively suppressed early successional forest stages in many parts of the National Parks. The most recent large scale fire in the study area occurred in 1926 in the upper Kootenay valley in and adjacent to Kootenay National Park. It resulted in a mosaic of young and mature forest patches interspersed throughout the montane spruce landscape. In contrast, Yoho National Park is dominated by a homogeneous matrix of late successional forests.

3.0 Methods

The study was divided into four parts (Figure 3). First, a common scale and common format GIS database was created using forest inventory data, biophysical habitat maps, aerial photographs, and bird point count locations. Second, a patch classification system was developed to create landscape maps of the montane spruce zone for the years 1953, 1973, 1978, 1983, 1988, and 1993. Third, several landscape indices were selected to quantify landscape structure. Finally, spatial and temporal landscape patterns were assessed and bird responses to surrounding habitat patterns were analysed.

1. DATA SOURCES AND MANAGEMENT

Create GIS database with forest inventory and biophysical habitat data
Map forest cover in protected areas using aerial photographs
Ground truth forest cover maps for KNP and YNP
Digitize and input KNP and YNP forest cover maps into GIS database
Input bird point count locations into GIS database

2. CREATE LANDSCAPE MAPS

Develop patch and edge classification systems
Create landscape map from forest cover maps
Stratify landscape map by biogeoclimatic subzones
Reconstruct historical landscape maps (1953-1993)

3. SELECT INDICES TO QUANTIFY LANDSCAPE STRUCTURE

Select indicators of landscape structure (composition and configuration)

4. DATA ANALYSIS

Spatial and temporal analysis of landscape patterns
Characterize managed and protected landscape patterns
Describe changes in managed forest landscape patterns since 1953

Describing bird responses to surrounding habitat pattern
Quantify habitat pattern surrounding bird point count locations (50-1000 m radius)
Develop regression models describing bird responses to surrounding habitat pattern
Assess the effects of spatial extent on habitat models

Figure 3: Description of the data layers and steps followed during the analysis.

3.1 Data Sources and Management

The study relied on four main sources of spatial and attribute data: (1) digital forest inventory data, (2) biophysical habitat maps, (3) aerial photographs, and (4) bird point count data. The maps and aerial photographs were current to 1991 for the entire study area and updated to 1993 to match the date of the bird survey. All spatial and attribute data were input and stored in TERRASOFT, a vector-based GIS, and Microsoft FOXPRO, a database management system.

Forest Inventory Data

Seven 1:20,000 digital forest cover maps of the managed landscapes along with their attribute databases were obtained from the Inventory Branch of the B.C. Ministry of Forests (MOF) in Victoria. The forest cover maps were produced from a combination of aerial photographs, field surveys, and satellite imagery to assist in the planning and management of British Columbia's public forest lands. Topographical data and logging roads were not available with all map sheets and consequently were not used. The forest cover layer was the primary layer used during the analysis. This layer includes information on the location and spatial arrangement of forest and non-forest stands. The associated attribute databases contain non-spatial data on stand and timber characteristics. Three attributes were used in this study: leading tree species, stand age, and crown closure.

The Forest Inventory Manual (B.C. MOF 1992) specifies a certain level of accuracy for all attributes measured as part of the forest inventory process. The specified accuracy for species composition is 85% for the correct order of dominant species while age class and crown closure class are specified to be within one class 85% of the time. The achieved accuracy of the forest attribute data has been estimated at 70-85% for species composition, 80-85% for age class, and 95% for crown closure (Leckie and Gillis 1995).

Biophysical Habitat Maps

Two digital biophysical habitat maps (1:100,000-250.000) of the North Columbia Mountains were obtained from the B.C. Ministry of Environment, Lands and Parks through B.C. Hydro. The maps were used to extract information on the distribution of biogeoclimatic subzones in the study area.

Aerial Photographs

The forest cover maps obtained from B.C. MOF do not include the areas of Yoho and Kootenay National Parks that are located within the study area. These areas are managed by the National Parks Service which uses an ecological (biophysical) land classification system. This hierarchical system integrates information on landform, soil and vegetation into ecosite units at a scale of 1:50,000. Potential vegetation types are described for each ecosite but their location and areal extent – critical components of this study – are not mapped. Consequently the ecosite maps were not used and forest cover was mapped using a set of medium scale black and white panchromatic aerial photographs that were acquired from MAPS B.C.

The photographs were of the same scale (1:15,840) and flown in the same year (1991) as those used in the adjacent managed forest lands. The forest cover of Yoho and Kootenay National Parks was mapped following the protocol established by B.C. Ministry of Forests (B.C. MOF 1992). The procedure consisted of four steps. First, relatively homogeneous forest and non-forest polygons were delineated onto a mylar overlaid on aerial photograph stereopairs. Second, the leading tree species, seral condition, and crown closure class for each forest polygon were identified. Non-forest polygons were classified into one of 6 habitat types: shrublands, grasslands, wetlands, rock, alpine, and rivers/lakes. Third, the polygons were digitized and attributes were entered into a database management system. The resulting map was then merged with the other 7 map sheets representing the managed forest landscape. Fourth, the forest cover maps for Yoho and Kootenay National Parks were ground truthed in May 1994. Forest and non-forest attribute accuracy was estimated to be 95% and 88% respectively for polygons lying in the dry cool montane spruce (MSdk) subzone (Appendix 1). The minimum mapping unit was approximately 5 hectares for forest polygons and 2 hectares for non-forest types (MOF 1992). The minimum width of a polygon was 50-100 metres. The MSdk subzone was mapped for both protected areas. The Engelmann spruce – subalpine fir (ESSF) subzones in the parks were only partly interpreted (approximately one third of the ESSF) due to the lack of coverage of the photographs and the difficulty of interpreting forest cover in steep topography.

Bird Survey

A survey of birds in the Beaverfoot and Kootenay valleys was completed in the spring and summer of 1993 by the Centre for Applied Conservation Biology of the University of British Columbia. The survey was part of a research project funded by Parks Canada to assess the effects of forest practices on biodiversity at the stand and landscape levels (Galindo-Leal 1994). The bird survey was conducted in the dry cool montane spruce (MSdk) subzone in the managed and protected areas. Stand-level habitat attributes were also measured at each bird point count location.

Birds were surveyed using fixed radius point counts (circular sampling units with a radius of 100 m) located along transects. The transects were placed: (1) inside continuous forest habitat in Kootenay and Yoho National Parks, (2) inside clearcuts in the managed forest lands, (3) across high contrast clearcut/forest edges in the managed forest lands, and (4) inside remnant forest habitats (and corridors) in the managed forest lands. A total of 117 point counts were located along 39 transects (Appendix 2). Each transect contained three point count locations, generally within 200 m of each other. Most point counts were repeated four times between May and July 1993. Counts lasted 10 minutes and birds were identified by sight and sound. The approximate location of birds within the sampling unit was recorded. Total number of individuals, species richness, and Shannon diversity index were calculated for each location. Common names, scientific names, and codes for bird species included in the analyses are listed in Appendix 3.

The bird abundance data used in this study is subject to several sources of bias that may affect the precision and accuracy of the results (Bibby 1992). First, the bird survey was undertaken by two different observers resulting in potential bias due to differences in personal experience, motivation, and hearing. Observer bias was minimized by training observers prior to the survey and by distributing each observer's effort among sample points over the four visits. Second, the detectability of bird species may vary due to several factors. For instance, detectability may vary between habitats: more species may be detected in clearcuts than in mature forests simply because birds are more audible and visible. In this survey, detectability of almost every species was similar between habitats (Galindo-Leal 1994). Detectability may also vary as a function of species (i.e., some species are more visually or aurally conspicuous than others), density, and activity. It is possible that some bird species may have been under-represented or not detected at all. Finally, several extraneous factors such as highway noise, creek noise, and mosquitoes posed some difficulty during the counts.

3.2 Creating Landscape Maps

Forest cover maps, biophysical habitat maps, and aerial photographs were used to produce a landscape (habitat patch) map of the montane spruce (MS) biogeoclimatic zone the Beaverfoot study area for the year 1993 (Table 1). Eight habitat patch types were defined, including 5 forest patch types and 3 non-forest patch types. Forest types varied on the basis of stand age and crown closure. Leading tree species were excluded from the classification system to reduce the number of habitat types used in subsequent analyses. Non-forest types included upland (grassland, shrubland, clearing, rock) wetland (e.g., swamp), and water (rivers and streams).

Table 1: Description of habitat patch types occurring in the montane spruce zone.*

Code	Patch type	Description
Patch Classification (8 patch types)		
CCUT	Recent disturbance	0 - 25 years since logging or burning (early-seral)
YOUN	Young coniferous forest	26 - 80 years since last disturbance (mid-seral)
OMAT	Open mature coniferous forest	10 - 25% crown closure; 81+ years (late-seral)
CMAT	Closed mature coniferous forest	26 - 100% crown closure; 81+ years (late-seral)
DECI	Deciduous forest	Aspen and balsam poplar forests
UPLD	Upland non-forested opening	Upland shrub, herb; rock/cliff; clearings
WTLD	Wetland non-forested opening	Wetland shrub, herb
WATR	Water	Rivers and lakes
Patch Classification (4 patch types)		
CCUT	Recent disturbance	0 - 25 years since logging or burning (early-seral)
YOUN	Young coniferous forest	26 - 80 years since last disturbance (mid-seral)
MATU	Mature coniferous forest	81+ years since last disturbance (late-seral)
NONF	Non forest patch type	DECI, UPLAND, WTLD, WATR

*Two classification systems are used depending on the type of analysis (see text). The 4 patch type classification system is a generalization of the 8 patch type classification system.

Several steps were required to create the habitat patch map. First, the B.C. MOF digital forest cover maps were 'cleaned up' in TERRASOFT to fix problems with some of the forest cover polygons such as dangles, slivers, and missing or incorrect labels. The 7 map sheets were then merged together and updated to 1993 using B.C. MOF paper maps showing the location and spatial extent of recent clearcuts. This map was merged with the two forest cover maps interpreted from the 1991 aerial photographs of Kootenay and Yoho National Parks to create a seamless coverage for the year 1993; it was assumed that no major stand replacing disturbance occurred in the two protected areas between 1991 and 1993. The biogeoclimatic subzone coverages from the biophysical habitat maps were also ‘cleaned up’ to fix minor problems such as dangles and slivers.

Four raster map layers were then generated from the forest cover and biogeoclimatic coverages: leading tree species, stand age, crown closure, and biogeoclimatic subzones. The raster map layers were then exported to IDRISI (Eastman 1992), a grid-based GIS, for spatial analysis. The leading tree species, stand age, and crown closure layers were each overlayed with the biogeoclimatic subzone layer to stratify the study area into biogeoclimatic subzones thus controlling for climate, soil, vegetation, and elevational variability. Only the MS zone was further considered during the analysis. The stand age and crown closure layers were then overlayed and reclassified to create a landscape map for the MS zone with 8 types (Table 2). The MS landscape map was then divided into four landscape units: (1) YNP = Yoho National Park (2388 ha); (2) KNP = Kootenay National Park (4957 ha); (3) NWBF= the northwest portion of the managed landscape adjacent to YNP (7152 ha); and (3) SEBF = the southeast portion of the managed landscape adjacent to KNP (4967 ha). This was done (1) to reduce the size of the managed landscapes in comparison to the protected landscapes and (2) to control for the effects of a wildfire which burned through the SEBF and KNP units in 1926.

A set of historical habitat maps (i.e., 1953, 1973, 1978, 1983, and 1988) were reconstituted using the 1993 rasterized stand age coverage. It was assumed that there were no large scale stand replacing disturbances in the MS zone other than logging during this time period. This assumption appears tenable based on discussions with B.C. MOF staff, the examination of forest cover maps, and the date of establishment of fire suppression policies in the early part of this century. Only four patch types were used to minimize polygon misclassification: recent disturbance, young forest, mature forest (open and closed mature forest), and non-forest (upland, wetland, and water). Each map was created by: (1) subtracting the appropriate number of years from the 1993 raster file and (2) reclassifying the age map into 3 age classes (0-25 yrs, 26-80 yrs, 81+ yrs). If a clearcut became a non-clearcut, it was assigned the attribute of the surrounding matrix of dominant patch type (i.e., young or mature forest type). Non-forest types were not modified.

Table 2: Characteristics of landscape (habitat patch) maps used in the spatial and temporal landscape analyses and the bird-habitat analysis.

Characteristic	Spatial Pattern Analysis	Temporal Pattern Analysis	Bird-Habitat Analysis
Number of landscape units	4^a	6^b	8^c
Grain (non-forest / forest)	2 ha / 5 ha	2 ha / 5 ha	2 ha / 5 ha
Extent (range)	2387.5 - 7151.5 ha	12118.8 ha	0.8 - 314.2 ha
Pixel size	0.25 ha	0.25 ha	0.25 ha
Number of patch types (max.)	8	4	4

(a) Two protected and two managed landscape units in 1993.
(b) The managed landscape unit in 1953, 1973, 1978, 1983, 1988, and 1993.
(c) Eight different-sized concentric circles around each of 117 bird point count locations.

3.3 Indices to Quantify Landscape Structure

Nineteen indices were selected to characterize landscape structure (Table 3). The indices were chosen because: (1) they are commonly used in landscape ecological studies (e.g., Ripple 1991, Li and Reynolds 1993, Pearson 1993), (2) they quantify different aspects of landscape composition and configuration, and (3) they are readily calculated using available computer software. Some of the metrics quantify attributes of a particular patch type (e.g., young forest patch type) while others measure attributes of the landscape as a whole (e.g., contagion). Patch type metrics can be broadly interpreted as fragmentation indices while landscape metrics can be interpreted as measures of spatial heterogeneity (McGarigal and Marks 1993).

Total landscape area (ha) is simply the areal extent of each landscape unit. It varied with the type of analysis performed (Table 3). *Percent patch type* (%) measures the percentage of the landscape occupied by each patch type. This is the sum of the area occupied by each patch in a particular patch type. Eight patch types were used for the spatial pattern analysis while four patch types were used for the temporal pattern analysis and bird habitat analysis (Table 2). *Percent mature core habitat* (%) measures the percentage of the landscape occupied by mature forest interior (core) habitat. Interior habitat was calculated by subtracting a 150 m wide buffer along the perimeter of each mature forest patch (Franklin and Forman 1987, Morrison 1990, Morrison *et al.* 1990). *Percent edge habitat* (%) measures the total percentage of mature forest patch type that is edge habitat. Edge habitat was calculated by subtracting percent mature forest interior habitat from percent mature forest patch type patch.

Table 3: Acronyms and names of landscape indices along with the part of the analysis in which they were used. Indices are described in the text.

Acronym	Index Name	Spatial Pattern Analysis	Temporal Pattern Analysis	Bird Habitat Relations
LAND	Landscape unit area (ha)	yes	yes	yes
PATCH	Percent of landscape (%)	yes	yes	yes
CORE	Core area percent of landscape (%)	yes	yes	yes
EDGE	Edge area percent of landscape (%)	yes	yes	yes
LPI	Largest patch index (%)	yes	yes	-
LCAI	Largest core area index (%)	yes	-	-
NP	Number of patches	yes	yes	-
NCA	Number of core areas	yes	yes	-
PD	Patch density (#/km^2)	yes	yes	-
CAD	Core area density (#/km^2)	yes	yes	-
PR	Patch richness	yes	yes	-
SIDI	Simpson's patch diversity index	yes	yes	yes
MPS	Mean patch size (ha)	yes	yes	-
PSSD	Patch size standard deviation (ha)	yes	yes	-
MCA	Mean core area (ha)	yes	yes	-
CASD	Core area standard deviation (ha)	yes	yes	-
FRACT	Fractal dimension	yes	yes	-
HCED	High contrast edge density (m/ha)	yes	yes	yes
CONTAG	Contagion index (%)	yes	yes	-

Largest patch index (%) measures the percentage of the total area of the landscape occupied by the largest patch of each corresponding patch type. A patch type dominated by one contiguous patch will have a high largest patch index whereas a highly fragmented patch type will have a low index. *Largest core area index* (%) was used in the same way to measure the percentage of the landscape occupied by the largest core area. *Number of patches* and *number of core areas* measure the number of patches of a particular patch type and the number of core areas, respectively. The number of core areas can often be greater than the number of mature forest patch types. For example, a single mature forest patch resembling the figure 8 can be divided into 2 core areas when the 150 m buffer zone is subtracted. *Patch density* (#/100 ha) is the density of patches of one patch type per 100 ha. *Core area density* (#/100 ha) is the density of mature forest core areas per 100 ha.

Patch richness refers to the number of patch types present in the landscape, the maximum being either 4 or 8 patch types, depending on the analysis. *Patch diversity* is a measure of the number of patch types and their relative proportion in the landscape. It was calculated using Simpson's diversity index:

$$SIDI = 1 - \sum_{i=1}^{m} P_i^2$$

where P_i is the proportion of the landscape occupied by patch type *i* and *m* is the number of patch types present in the landscape. Simpson's index represents the probability that two randomly selected patches belong to different patch types. Relatively more weight is given to common patch types than to rare patch types (Krebs 1989).

Mean patch size (ha) was used to measure the average size of all of the patches within a patch type:

$$MPS = \frac{\sum_{j=1}^{n} a_{ij}}{n_i}\left(\frac{1}{10{,}000}\right)$$

while *patch size standard deviation* (ha) was used to measure patch size variability:

$$PSSD = \sqrt{\frac{\sum_{j=1}^{n}\left[a_{ij} - \left(\frac{n\sum_{j=1} a_{ij}}{n_i}\right)\right]^2}{n_i}}\left(\frac{1}{10{,}000}\right)$$

where a_{ij} is the area (m^2) of patch *ij* and n_i is the number of patches in the landscape of patch type *i*. *Mean core area* (ha) and *core area standard deviation* (ha) measure core area size and variability, respectively, using the preceding two formulas.

Patch shape was measured using fractal analysis, which is based on patch perimeter-area relations. *Fractal dimension* measures the complexity of patch size and shape relations:

$$FRACT = \frac{2}{\dfrac{\left[n_i \sum_{j=1}^{n} (\ln p_{ij} \circ \ln a_{ij})\right] - \left[\left(\sum_{j=1}^{n} \ln p_{ij}\right)\left(\sum_{j=1}^{n} \ln a_{ij}\right)\right]}{\left(n_i \sum_{j=1}^{n} \ln p_{ij}^2\right) - \left(n_i \sum_{j=1}^{n} \ln p_{ij}\right)^2}}$$

where p_{ij} is the perimeter (m) of patch *ij*, a_{ij} is the area (m^2) of patch *ij*, and n_i is the number of patches in the landscape of patch type *i*. Fractal dimension is estimated by using the method of successive linear regression of $\log(A_k)$ against $\log(P_k)$ where D equals twice the slope of the regression line (McGarigal and Marks 1993). Fractal dimension values range from 1 to 2. Values near 1.0 indicate a simple shape approaching a circle, whereas values near 2.0 describe extremely complex shapes.

High contrast edge density (HCED) measures the density of edges between mature forest patch types and clearcuts or other non-forest vegetation types:

$$HCED = \frac{\sum_{k=1}^{m'} (e_{ik} \circ d_{ik})}{A}$$

where e_{ik} is the total length (m) of edge in the landscape between patch types *i* and *k*, d_{ik} is the dissimilarity (edge contrast weight) between patch types *i* and *k*, and A is the total landscape area (m^2). A binary edge contrast matrix (dissimilarity matrix) was developed to calculate high contrast edge density (Appendix 4). High contrast edges were defined on the basis of large structural differences between mature forest patches and adjacent patch types as determined from forest cover maps and aerial photographs. Boundaries between mature forest patch types and clearcuts or non-forest types received a weight of one. All other boundaries received a weight of zero.

Finally, *contagion* measures the extent to which all habitat patches in a landscape are aggregated or clumped:

$$CONTAG = \left[1 + \frac{\sum_{i=1}^{m} \sum_{k=1}^{m} \left[(P_i) \left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}} \right) \right] \circ \left[\ln(P_i) \left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}} \right) \right]}{2\ln(m)} \right] (100)$$

where P_i is the proportion of the landscape occupied by patch type I, g_{ik} is the number of adjacencies (joins) between pixels of patch types i and k, and m is the number of patch types present in the landscape. A landscape with a few large, contiguous patches has a higher contagion value than one with many small, dispersed patches.

3.4 Data Analysis

Spatial and Temporal Analysis of Landscape Patterns

FRAGSTATS (McGarigal and Marks 1993), a spatial pattern analysis program, was used to calculate most of the metrics. Patch type and landscape variables were summarized in tables and graphs to facilitate the comparison of landscape structural patterns between managed and protected landscapes and over time periods. Confidence intervals were provided only for metrics which quantify an average patch value. Other metrics, such as contagion and Simpson's patch diversity, which characterize the landscape as one unit, do not have confidence intervals. Moreover, statistical tests which compare landscapes in time and space are not necessary or possible because the entire study area is being quantified and not just a sample of it.

Bird Responses to Surrounding Habitat Pattern

Multiple regression analysis was used to develop habitat models for three bird community variables (species richness, species diversity, and total abundance) and several bird population variables (relative abundance of bird species). Habitat pattern variables in concentric circles around each bird point count location were measured using the habitat patch map (4 patch types) for 1993. Eight concentric circles of increasing radius were used: 50 m (0.8 ha), 100 m (3.1 ha), 150 m (7.1 ha), 200 m (12.6 ha), 250 m (19.6 ha), 500 m (78.5 ha), 750 m (176.7 ha), and 1000 m (314.2 ha). Because of the 50-m grid cell size, it was not possible to use a radius of less than 50 m. Seven variables were selected to characterize the composition of the habitat mosaic surrounding bird point count locations (Table 4). Some metrics, such as the contagion and nearest-neighbour indices were not used because the concentric circles were too small and contained too few patches for the metrics to be meaningful.

Table 4: Bird response and landscape variables used to develop stepwise regression models.

Bird Response Variables	
Community Variables	
TOTN	Total abundance of individuals.
NSPP	Species richness (number of species).
SHDI	Shannon's diversity index.
Population Variables	
"BIRD"	Abundance of individual species.
Landscape Variables (neighbourhood scale)	
CCUT	Percentage of recently disturbed forest (0-25 yrs).
YOUN	Percentage of young forest (26-80 yrs)).
CORE	Percentage of mature interior forest habitat (81+ yrs).
EDGE	Percentage of mature edge forest habitat (81+ yrs).
NONF	Percentage of non-forest habitat.
HCED	Density of high contrast edge (m/ha).
SIEI	Simpson's evenness index.

A total of 936 circular habitat maps were produced (eight concentric circles around each of 117 point count locations). Several batch files were created to facilitate the process of creating the circular habitat maps in IDRISI, calculating the habitat variables using FRAGSTATS, and extracting the appropriate subset of patch type and landscape metrics for statistical analysis. SYSTAT (Wilkinson 1992) was then used to develop the regression models.

Univariate and Bivariate Analysis

Bird species diversity and relative abundance in the 117 plots were calculated for each habitat and edge type (i.e., mature forest, young forest, clearcut, young / clearcut edge, and mature / clearcut edge). Means and standard deviations for habitat neighbourhood variables were also calculated for each of the eight concentric circles. The relations between bird response variables and habitat neighbourhood variables and among habitat neighbourhood variables were then examined for the 19.6 ha concentric circles (habitat neighbourhoods) by means of correlation matrices. Among the 8 different-sized circles, the 19.6 ha circle represented a balance between relatively strong relations and relatively low standard errors. Only the 10 bird species included in regression analyses were included in the correlation matrix. Bonferroni-adjusted probabilities were calculated to test the statistical significance of the Pearson correlation coefficients among the variables ($\alpha = 0.05$). Highly correlated variables (i.e., $r > 0.80$) were removed prior to the stepwise multiple regression analysis (Wilkinson 1992).

Multiple Regression Analysis

Several statistical methods can be used to develop predictive models which estimate the presence or abundance of a species given one or more habitat variables (Morrison *et al.* 1992). Multiple regression analysis was selected because both dependent and independent variables are continuously distributed (i.e., each regression model can focus on how a particular species' abundance is related to habitat variables). In particular, stepwise regression analysis was used to develop predictive models relating one dependent variable to one or more independent variables (model building) and not to test hypotheses (model testing). This approach to regression analysis, a form of "exploratory data analysis", was chosen because there is no strong theoretical basis for using any or a specific set of landscape variables. The large number of regression models being developed (936 models) also precluded a more interactive approach to regression analysis (Tabachnick and Fidell 1989).

Models were developed for three bird community variables and for all bird species which were present in at least seven different plots (i.e., equal to or greater than the number of independent variables) (Kozak 1995, personal communication). In total, 22 out of 69 bird species were initially included in the analysis. No accurate estimates of the regression coefficients were given due to the large number of significance tests performed (unreliable p values). All of the data were used to develop the models rather than splitting the data into a model building and model validating phase. A recommended ratio of 10-20 observations to 1 independent variable was thus maintained (Tabachnick and Fidell 1989). Keeping the ratio of predictor variables to sample size low allows the development of the strongest possible models and avoids model prediction bias (i.e., optimistically high model R^2) (Verbyla and Chang 1994). The data set was not divided to eliminate the possibility of not being able to validate the models due to the relatively low sample sizes (i.e., reduced degrees of freedom) of each set.

All habitat pattern variables with a significant p value ($p \leq 0.05$) were included in the regression models (Wilkinson 1992). The multiple coefficient of determination (R^2) and the standard error of the estimate (SEy) were used to measure the strength and significance of the regression models. R^2 measures the proportion of the variation in the independent variables associated with the variation in the dependent variable. SEy measures the scatter or spread of actual Y values around the regression line (i.e., the predicted Y values).

Several assumptions underlie regression analysis (Hamilton 1992): (1) independent variables have fixed values, (2) errors have zero mean, constant variance, are uncorrelated with each other, and are normally distributed, and (3) no important variables are excluded since their omission may produce spurious results. The first assumption is partly realized because habitat pattern variables can be measured repeatedly using a GIS to obtain the same values. However, it may not be possible to recreate identical forest cover maps due to several sources of error including inter-observer variability (i.e., due to aerial photo interpretation and subsequent ground truthing) and digitizing error. The distributional assumptions were checked by calculating regression diagnostics with the computer program EASYREG (Marshall *et al.* 1995). Regression diagnostics were performed for each community and population habitat model.

Non-normality, heteroscedasticy, and autocorrelation tests did not reveal any problems for the three community-habitat models. Conversely, only two out of the 10 population-habitat models, those for the Golden-crowned Kinglet and Swainson's Thrush, were without problems. The other 8 models were all plagued by residual errors which were not normally distributed according to the K-square test for non-normality. Because the sample was large (n=117), violating the non-normality assumption probably does not have serious consequences on the regression models (Hamilton 1992, Marshall *et al.* 1995). Nonetheless, a variety of variable transformations (dependent and independent variables) were attempted to rectify the problem. None of the transformations resulted in a normal error distribution indicating that the relation between the abundance of these species and surrounding habitat pattern may in fact be non-linear.

4.0 Results

4.1 Characteristics of Managed and Protected Landscapes

Each managed and protected montane spruce landscape revealed different structural patterns as a result of variations in human activities and natural disturbances (Figure 4, Table 5). The YNP landscape has not been affected by any recent major disturbance and was characterized by an extensive and contiguous late-seral forest matrix. The NWBF landscape has been extensively logged and was characterized by a uniform arrangement of clearcuts embedded in a greatly reduced mature forest matrix. The SEBF landscape has been affected by both logging and a large wildfire (ca. 1926) resulting in two forest matrices: a mature forest matrix perforated by numerous clearcuts and a young forest matrix (which succeeded the wildfire) containing fewer and smaller clearcuts. The KNP landscape has also been affected by the 1926 wildfire and represented a heterogeneous mosaic of young and mature forest patches.

The landscape metrics were indicative of the overall spatial heterogeneity of a particular landscape while the patch type metrics were more indicative of the fragmentation of a particular habitat type (Table 5). The density of patches of all types was greater in the managed landscapes (NWBF = 3.66 patches/km^2; SEBF = 3.36 patches/km^2) than in the protected landscapes (YNP = 2.68 patches/km^2; KNP = 3.13 patches/km^2), although the difference between KNP and SEBF was relatively small. Lodgepole pine forests were most common in the NWBF and YNP landscapes while lodgepole pine and spruce/fir forests were equally abundant in the SEBF landscape. The proportion of spruce/fir forests in the YNP landscape coincided with the proportion of mature forest habitat.

Mature forest habitat (open and closed mature forest patch types) was dominant in the YNP and NWBF landscapes (88% and 61%, respectively) while young and mature forests were co-dominant in the KNP and SEBF landscape (39% and 32%, respectively, for SEBF; 39% and 53%, respectively, for KNP) (Figure 5b). Clearcuts (recent disturbance patch type) only occurred in the managed landscapes, comprising 29% and 18% of the NWBF and SEBF landscapes, respectively. Open mature forest habitat (<25% crown closure) comprised less than 2% of each landscape. The proportion of non-forest habitat varied between 6% and 10%. It was highest in the YNP and lowest in the KNP landscape.

The proportion of core habitat (mature forest interior habitat) was much higher in the protected landscapes than in the managed landscapes, representing 73%, 42%, 25%, and 13% of the YNP, KNP, NWBF, and SEBF landscapes, respectively (Figure 5c). Conversely, edge habitat (mature forest edge habitat) was more prominent in the managed landscapes, comprising 37%, 19%, 15%, and 11% of the NWBF, SEBF, YNP, and KNP landscapes, respectively. In addition, even though the NWBF landscape had more mature forest habitat than the KNP landscape, it had much less core habitat. High contrast edge density (the interface between closed mature forest and clearcut or non-forest patches) in the managed landscapes (NWBF = 42 m/ha; SEBF = 37 m/ha) was approximately two times greater than in the protected landscapes (KNP = 19 m/ha; YNP = 17 m/ha) (Figure 5c).

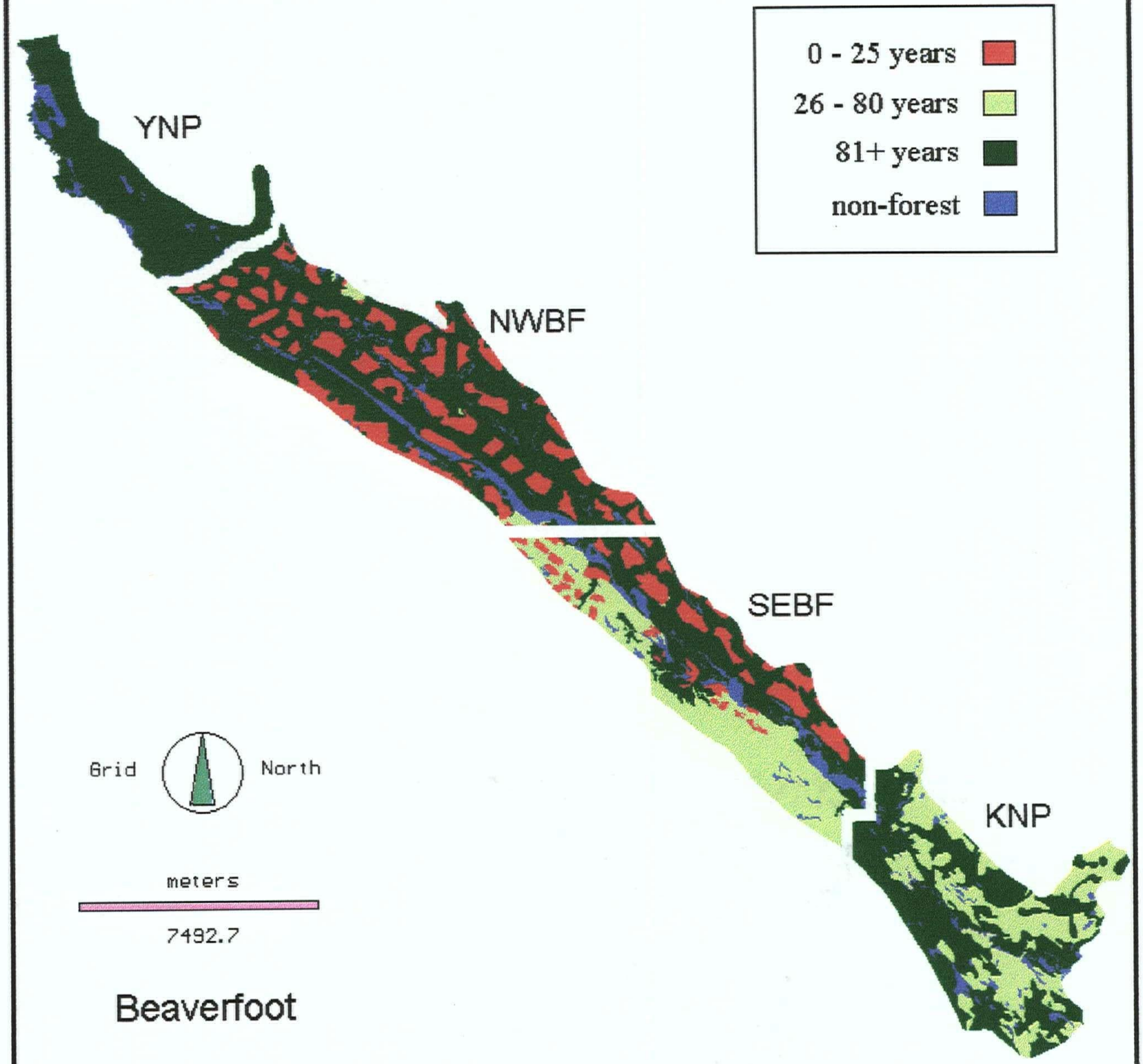
The fractal dimension index was used to measure the complexity of patch size and shape relations for the landscape as a whole. The YNP landscape (fractal dimension = 1.39) was the most complex of the landscapes while the NWBF landscape (fractal dimension = 1.28) is the least complex (Figure 6a). The SEBF and YNP landscapes had similar fractal dimension values, 1.35 and 1.37 respectively. Patch diversity, as measured by Simpson's diversity index, was highest in the SEBF landscape (0.71), followed by the KNP landscape (0.56), and lowest in YNP landscape (0.22) (Figure 6b). Patch diversity in the NWBF landscape (0.53) was similar to the KNP.

Table 5: Patch type and landscape metrics for managed and protected montane spruce landscapes in 1993.

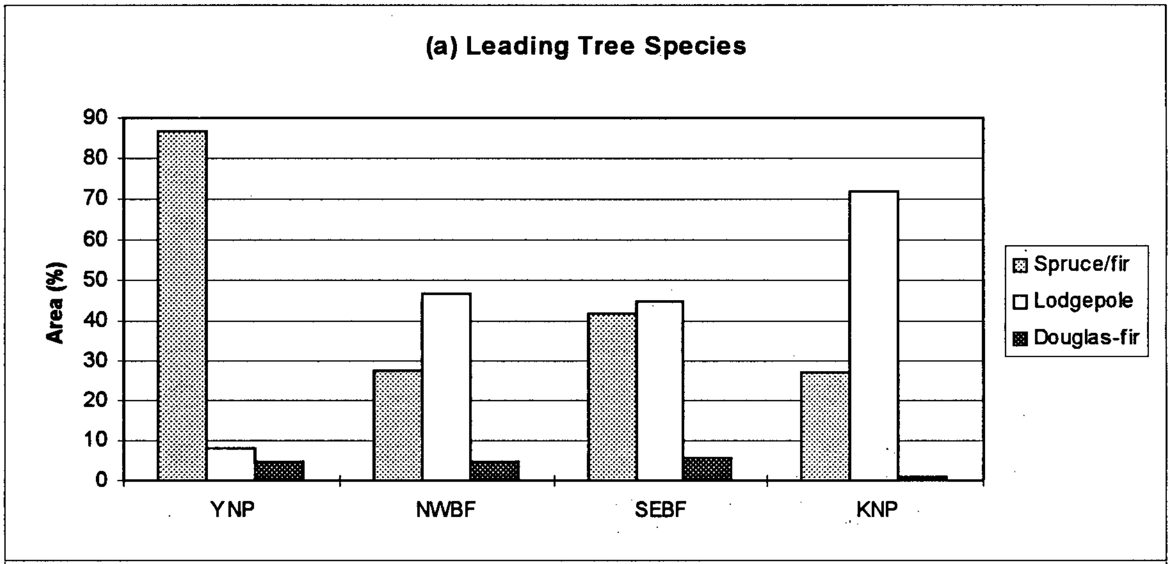
Landscape Metrics	YNP	NWBF	SEBF	KNP
Total landscape area (ha)	2387.50	7151.50	4967.25	4956.50
Number of patches (#)	64	262	167	155
Patch density (#/km^2)	2.68	3.66	3.36	3.13
High contrast edge density (m/ha)	16.84	41.68	37.28	19.01
Fractal dimension	1.39	1.28	1.35	1.37
Patch richness (#)	5	8	7	6
Patch diversity	0.22	0.53	0.71	0.56
Contagion (%)	78.66	65.32	52.08	59.19
Patch Type Metrics				
RECENT DISTURBANCE (0-25 years)				
Percent of landscape (%)	n/a	29.21	17.57	n/a
Largest patch index (%)	n/a	3.78	3.25	n/a
Number of patches (#)	n/a	59	42	n/a
Mean patch size (ha)	n/a	35.41	20.78	n/a
Patch size s.d. (ha)	n/a	39.75	30.12	n/a
Fractal dimension	n/a	1.20	1.22	n/a
YOUNG FOREST (26-80 years)				
Percent of landscape (%)	n/a	1.29	39.00	39.21
Largest patch index (%)	n/a	0.52	32.13	11.04
Number of patches (#)	n/a	6	11	18
Mean patch size (ha)	n/a	15.42	176.09	107.96
Patch size s.d. (ha)	n/a	14.03	455.43	168.59
Fractal dimension	n/a	1.21	1.37	1.48
OPEN MATURE FOREST (81+ years)				
Percent of landscape (%)	1.99	0.16	1.85	1.69
Largest patch Index (%)	1.53	0.07	0.59	0.42
Number of patches (#)	2	3	8	7
Mean patch size (ha)	23.75	3.83	11.50	12.00
Patch size s.d. (ha)	12.75	1.31	11.67	6.58
Fractal dimension	0.73	1.69	1.43	1.68
CLOSED MATURE FOREST (81+ years)				
Percent of landscape (%)	87.98	61.44	32.00	53.12
Largest patch index (%)	87.76	60.95	29.16	39.35
Number of patches (#)	3	13	11	12
Mean patch size (ha)	700.17	337.98	144.52	219.40
Patch size s.d. (ha)	986.47	1160.77	412.47	527.28
Fractal dimension	1.27	1.49	1.53	1.43
CORE HABITAT (150 m edge effect)				
Percent of landscape (%)	72.77	24.59	12.96	42.25
Largest core area index (%)	72.15	9.18	5.12	15.77
Number of core areas (#)	3	55	23	26
Core area density (#/km^2)	0.13	0.77	0.46	0.52
Mean core area (ha)	579.17	31.98	28.00	80.55
Core area s.d. (ha)	808.48	98.14	53.68	170.28
EDGE HABITAT (150 m edge effect)				
Percent of landscape (%)	15.20	36.84	19.04	10.86
NON-FOREST PATCH TYPES				
Percent upland patch type (%)	0.09	0.87	0.06	1.70
Percent wetland patch type (%)	6.98	4.63	8.68	2.74
Percent water patch type (%)	2.95	2.31	0.84	1.54

landscape. Patch richness, on the other hand, was highest in the NWBF landscape (8 patch types) and lowest in the YNP landscape (5 patch types). Contagion, indicative of the amount of clumping or aggregation of patches in a landscape, was highest in the YNP landscape (79%) followed by the NWBF (65%), KNP (59%), and SEBF (52%) landscapes (Figure 6c).

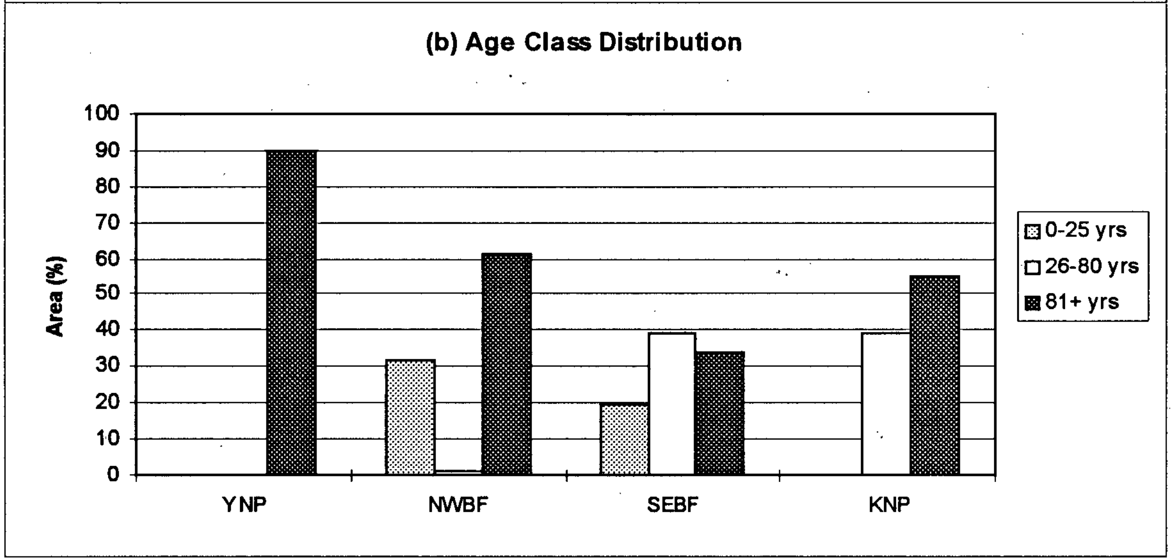
Figure 4: Managed and Protected Landscape Patterns in 1993



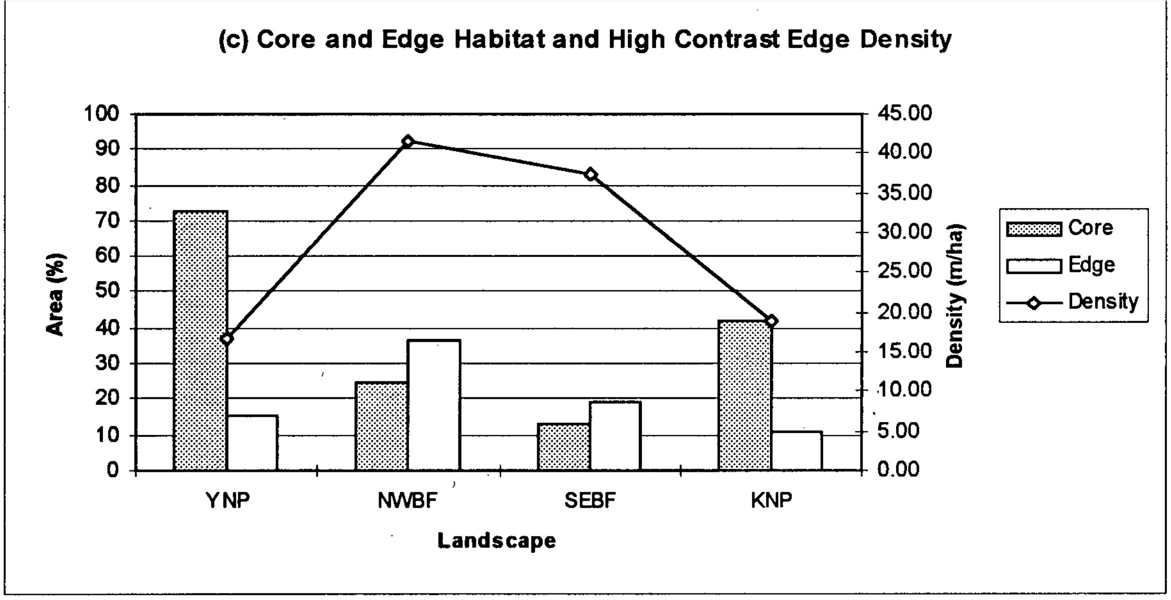
KNP = Kootenay National Park; NWBF = northwest managed Beaverfoot; SEBF = southeast managed Beaverfoot; YNP = Yoho National Park



(a) Leading Tree Species



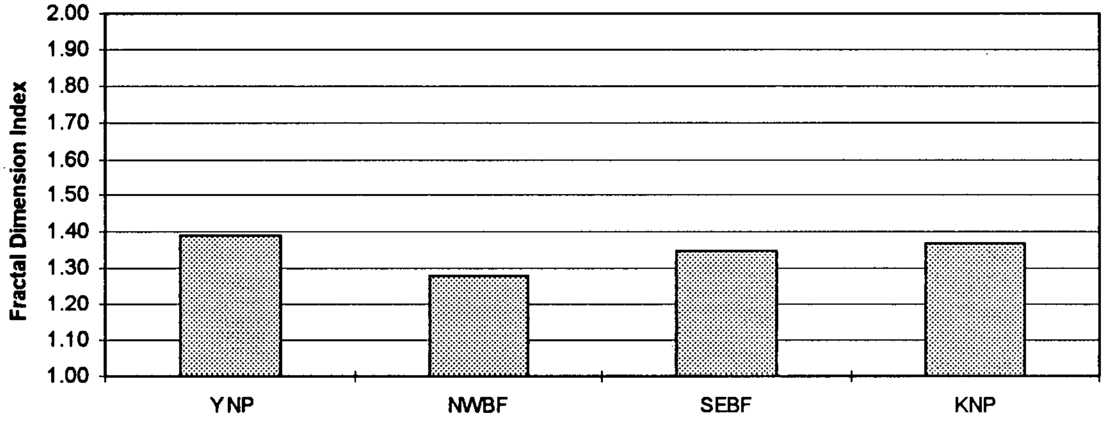
(b) Age Class Distribution



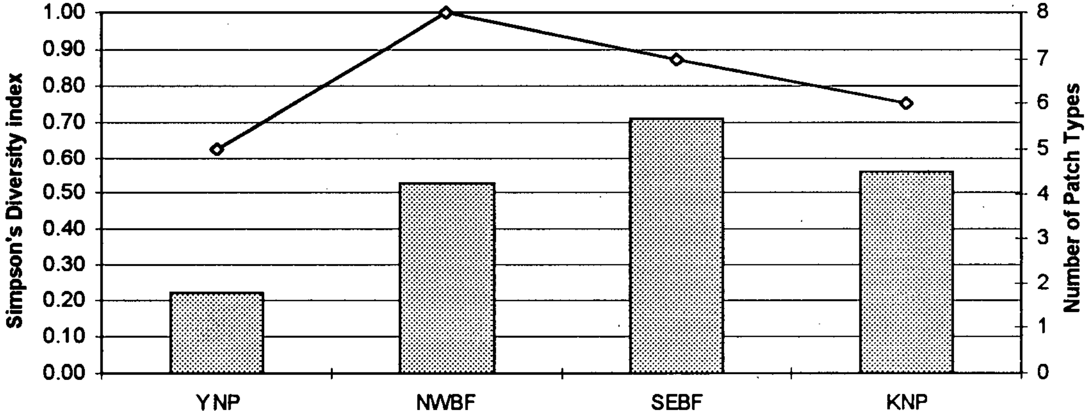
(c) Core and Edge Habitat and High Contrast Edge Density

Figure 5: Percent of each landscape by (a) leading tree species, (b), age class, and (c) core and edge habitat; high contrast edge density is also depicted in (c). YNP = Yoho National Park; NWBF = northwest managed Beaverfoot; SEBF = southeast managed Beaverfoot; KNP = Kootenay National Park.

(a) Patch Shape (Fractal Dimension)



(b) Patch Richness and Diversity



(c) Landscape Contagion

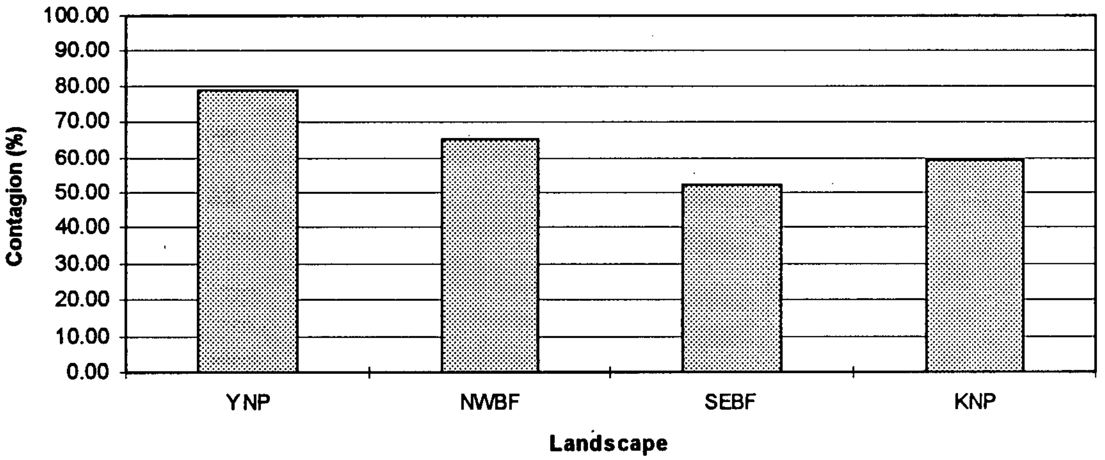


Figure 6: Metrics describing (a) patch shape (fractal dimension), (b) patch richness and diversity, and (c) landscape contagion for each landscape. See text for details. YNP = Yoho National Park; NWBF = northwest managed Beaverfoot; SEBF = southeast managed Beaverfoot; KNP = Kootenay National Park.

4.2 Temporal Changes in Managed Landscape Patterns

Clearcut logging has dramatically changed the structure of the managed montane spruce landscape during the past 40 years (Figure 7). The most rapid and extensive changes occurred between 1988 and 1993. Between 1953 and 1993, the number of clearcuts increased from 2 to 98 while the total area of clearcut habitat increased from 0.02% to 25% of the landscape (Table 6, Figure 8a). The majority of the clearcuts (60 clearcuts; 3,045 ha) were added in the period between 1988 and 1993. In contrast, during the past 40 years, mature forest habitat decreased in area from 72% to 50% of the landscape while the number of patches increased from 15 to 23. Mature forest patch area and size class distribution changed very little over time (Figure 10). The decrease in mature forest area was inversely proportional to the increase in clearcut habitat area and was also most pronounced between 1988 and 1993. Young forest habitat area was the least affected by past logging practices, decreasing in areal extent from 20% to 16% of the landscape. The number of young forest patches, though, more than doubled from 5 to 11.

The proportion of core habitat in the landscape decreased for each time period between 1953 and 1993 while edge habitat increased (Figure 8b). Total core area decreased from 62% of the landscape in 1953 to 32% in 1993. The number of core areas increased from 33 to 168 in the same time period. The greatest change occurred in the last 5 year interval when 87 new core areas were created. The amount of edge habitat was inversely related to changes in core habitat, decreasing in areal extent by approximately 50% since 1953. High contrast edge density, which was also inversely related to core habitat area, more than doubled in the past 40 years, from 16.3 m/ha in 1953 to 34.9 m/ha in 1993 (Figure 8b).

Patch diversity (Simpson's diversity index) increased steadily over time, from 0.44 in 1953 to 0.65 in 1993, reflecting the increasing heterogeneity of the landscape due to logging (Figure 8c). The total number of patches of all types also increased during the same period from 204 to

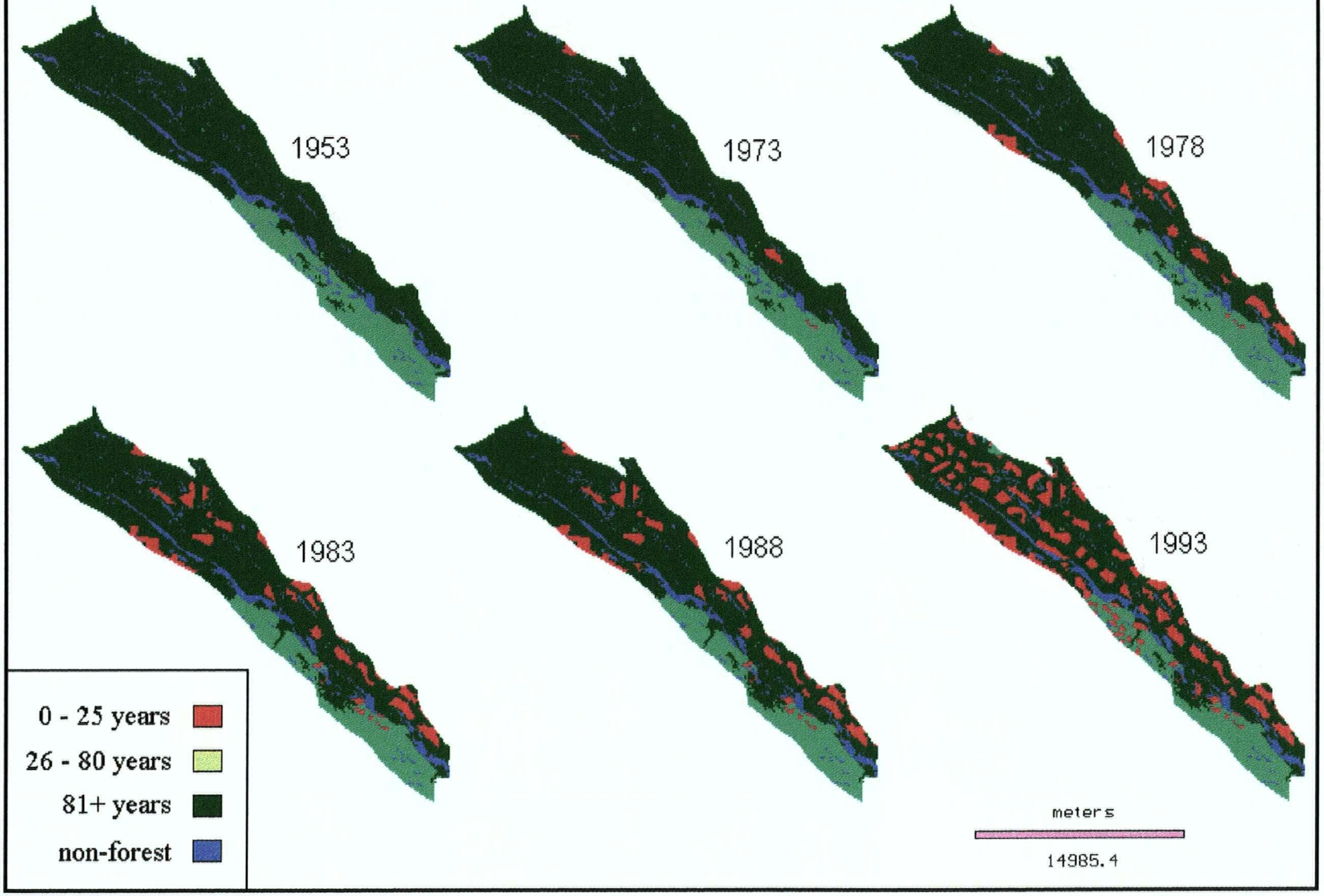
314 patches. Mean clearcut patch size varied between 31 ha and 37 ha from 1978 to 1993 (Figure 9a). Prior to 1978, mean clearcut size was 1 ha (2 patches) in 1953 and 23 ha (5 patches) in 1973. Clearcut patch size standard deviation followed the same pattern, increasing from 0.6 ha in 1953 (n = 2 clearcuts) to 35 ha in 1978 (n = 23 clearcuts) thereafter staying relatively constant (38 ha in 1993; n = 98 clearcuts). Mean patch size for young and mature forest patch types both decreased with time. Young forest patches decreased in mean size from 478 ha in 1953 to 177 ha in 1993, with the sharpest changing occurring between 1978 and 1983 when mean patch size decreased by 193 ha. Mean mature forest patch size, meanwhile, decreased from 579 ha to 265 ha in the same time period. The most rapid change occurred between 1988 and 1993 when mean patch size decreased by 249 ha. Patch size standard deviation also decreased steadily with time for both patch types. Young forest patch size standard deviation decreased from 951 ha in 1953 to 453 ha in 1993 while mature forest patch size standard deviation decreased from 2128 ha in 1953 to 1203 ha in 1993.

Patch shape was measured at the patch type and landscape levels (i.e., for all patch types combined). At the landscape level, fractal dimension decreased steadily from 1.44 in 1953 to 1.30 in 1983 (Figure 9b). At the patch type level, fractal dimension increased over time for mature forest patches (from 1.40 in 1953 to 1.48 in 1993), while changing very little for clearcut and young forest patches. In general the fractal dimension of the mature forest patches was higher than for young forest patches, although the difference was not always very large between 1953 and 1978. The fractal dimension of clearcuts was the lowest of all patch types (approximately 1.20). The fractal dimension of non-forest patches (1.48) was identical to mature forest patches in 1993. Finally, landscape contagion decreased over time from 64% in 1953 to 41% in 1993 (Figure 9c). As with most of the other indices used to characterize landscape structure, the most rapid change in contagion occurred in the last five year period.

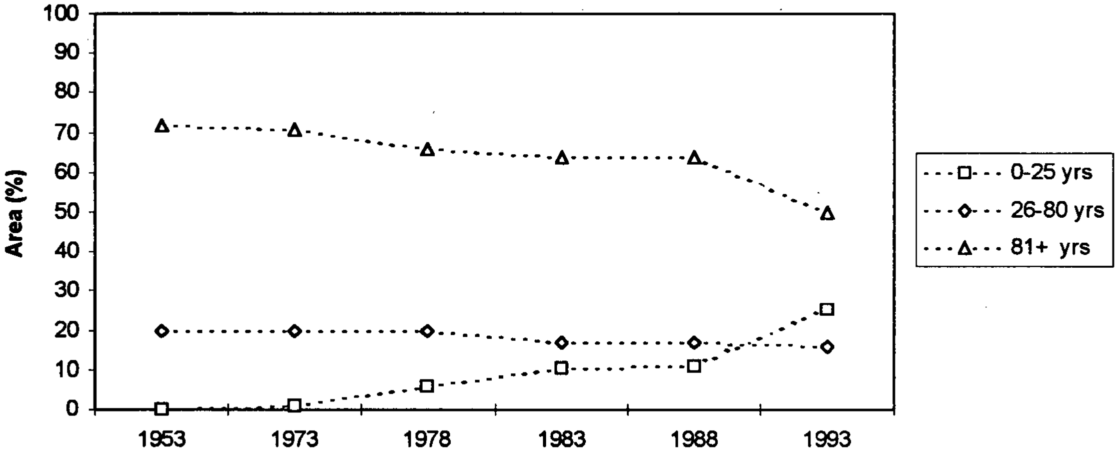
Table 6: Patch type and landscape metrics for the managed montane spruce landscape (NWBF + SEBF) for the years 1953, 1973, 1978, 1983, 1988, and 1993.

Landscape Metrics	**1953**	**1973**	**1978**	**1983**	**1988**	**1993**
Total landscape area (ha)	12118.75	12118.75	12118.75	12118.75	12118.75	12118.75
Number of patches (#)	204	208	229	242	245	314
Patch density (#/km^2)	1.68	1.72	1.89	2.00	2.02	2.59
High contrast edge density(m/ha)	16.30	16.97	20.54	24.59	25.04	34.89
Fractal dimension	1.44	1.43	1.39	1.36	1.36	1.30
Patch richness (#)	4	4	4	4	4	4
Patch diversity	0.44	0.45	0.52	0.54	0.55	0.65
Contagion (%)	64.10	61.88	54.76	51.27	50.85	41.39
Patch Type Metrics						
RECENT DISTURBANCE (0-25 years)						
Percent of landscape (%)	0.02	0.95	6.00	10.56	10.99	25.13
Largest patch index (%)	0.02	0.46	1.08	1.45	1.54	2.34
Number of patches (#)	2	5	23	35	38	98
Mean patch size (ha)	1.38	23.00	31.62	36.56	35.05	31.07
Patch size s.d. (ha)	0.62	19.28	35.26	41.53	41.39	38.02
Fractal dimension	1.20	1.18	1.19	1.21	1.21	1.20
YOUNG FOREST (26-80 years)						
Percent of landscape (%)	19.74	19.65	19.61	16.79	16.79	16.06
Largest patch index (%)	19.64	19.54	19.49	13.25	13.25	13.06
Number of patches (#)	5	6	6	10	10	11
Mean patch size (ha)	478.35	396.96	396.12	203.45	203.45	176.95
Patch size s.d. (ha)	950.83	881.25	879.39	482.83	482.83	453.31
Fractal dimension	1.38	1.37	1.38	1.32	1.32	1.39
MATURE FOREST (81+ years)						
Percent of landscape (%)	71.66	70.81	65.80	64.07	63.64	50.23
Largest patch index (%)	70.48	69.64	64.60	62.92	62.49	48.74
Number of patches (#)	15	15	18	15	15	23
Mean patch size (ha)	578.93	572.12	443.03	517.62	514.13	264.65
Patch size s.d. (ha)	2128.17	2102.67	1791.26	1899.58	1886.54	1202.95
Fractal dimension	1.40	1.41	1.41	1.44	1.45	1.48
CORE HABITAT						
Percent of landscape (%)	62.03	60.39	55.09	50.04	49.52	31.91
Number of core areas (#)	33	35	56	79	81	168
Core area density (#/km^2)	0.27	0.29	0.46	0.65	0.67	1.39
Mean core area (ha)	227.80	209.11	119.22	76.76	74.09	23.02
Core area s.d. (ha)	1045.40	986.30	682.46	506.45	492.58	172.79
EDGE HABITAT						
Percent of landscape (%)	9.63	10.42	10.71	14.03	14.12	18.32
NON-FOREST PATCH TYPES						
Percent of landscape (%)	-	-	-	-	-	8.58
Largest patch index (%)	-	-	-	-	-	1.74
Number of patches (#)	-	-	-	-	-	182
Mean patch size (ha)	-	-	-	-	-	5.72
Patch size s.d. (ha)	-	-	-	-	-	20.93
Fractal dimension	-	-	-	-	-	1.48

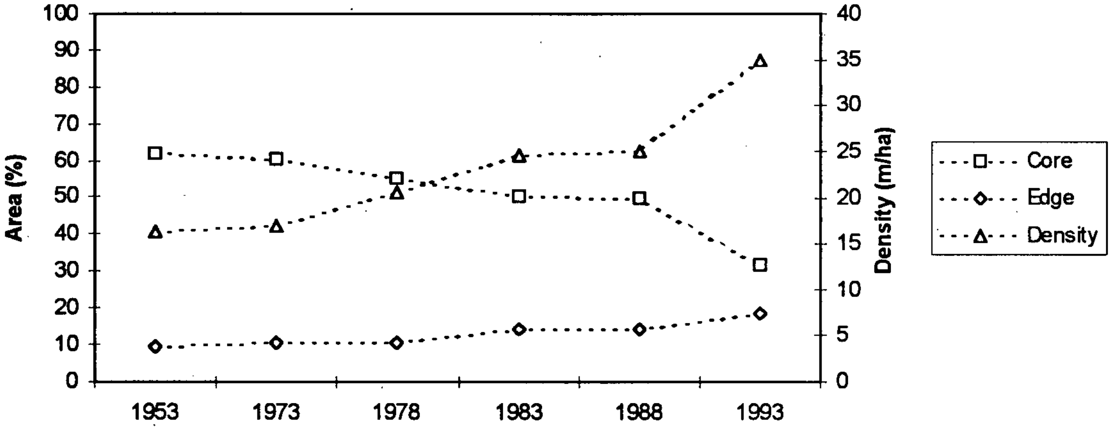
Figure 7: Temporal Changes in Managed Landscape Patterns (1953 -1993)



(a) Distribution of Early, Mid, and Late Seral Forest Patches



(b) Distribution of Core Habitat, Edge Habitat, and Edge Density



(c) Distribution of Patch Diversity and Total Number of Patches

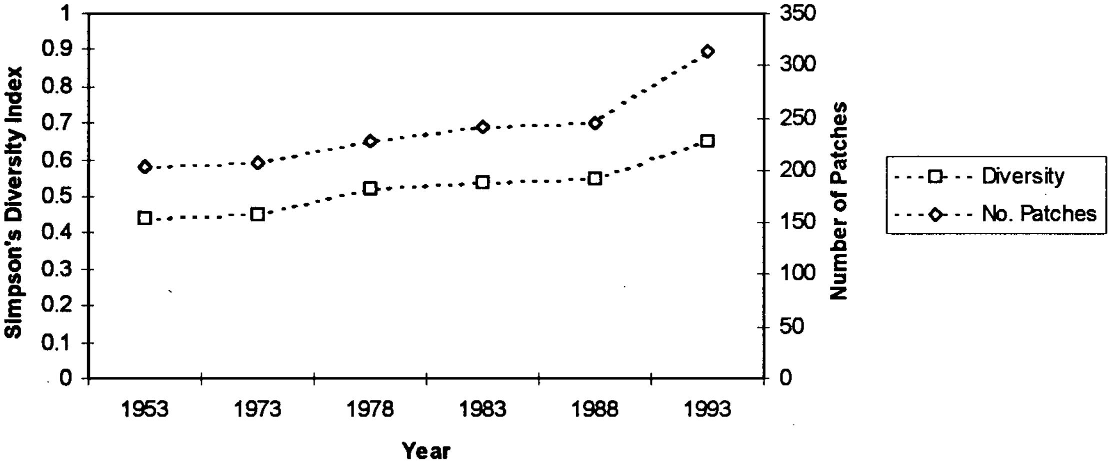
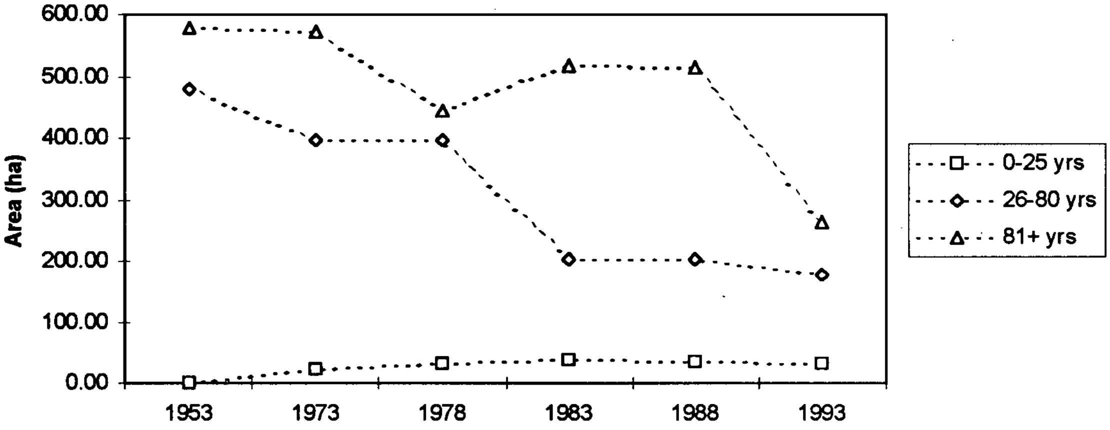
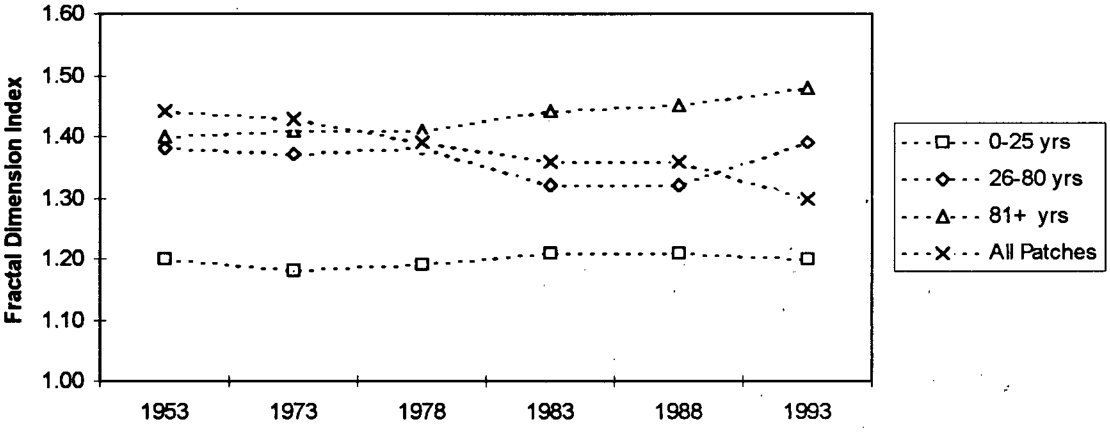


Figure 8: Temporal changes in the distribution of (a) early, mid, and late seral forest patches, (b) core habitat, edge habitat, and edge density, and (c) patch diversity and total number of patches.

(a) Distribution of Mean Patch Size



(b) Distribution of Patch Shape (Fractal Dimension)



(c) Distribution of Landscape Contagion

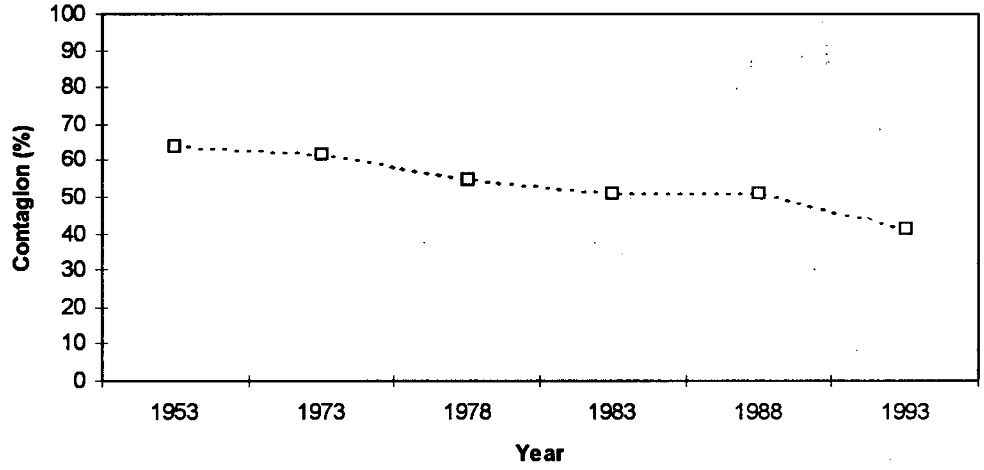


Figure 9: Temporal changes in the distribution of (a) mean patch size, (b) patch shape (fractal dimension), and (c) landscape contagion. See text for details.

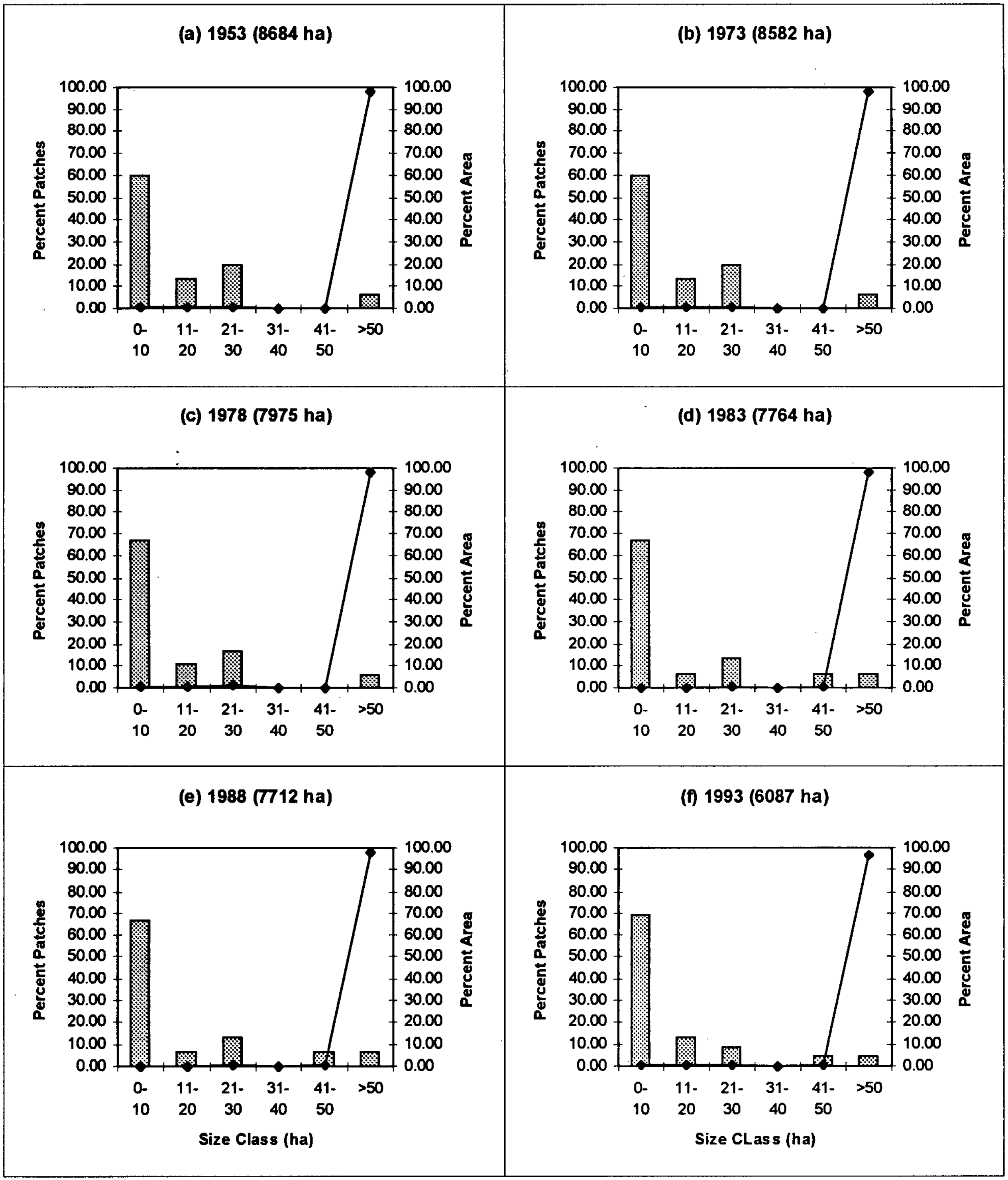


Figure 10: Mature forest patch area and size class distributions for (a) 1953, (b) 1973, (c) 1978, (d) 1983, (e) 1988, and (f) 1993.

4.3 Bird-Habitat Relationships

4.3.1 Univariate and Bivariate Analysis

Bird Community and Population Patterns

A total of 69 different bird species were recorded at 117 locations along 39 transects located in clearcuts, young forests, mature forests, young forest / clearcut edges, and mature forest / clearcut edges. Bird community variables – total bird abundance, species richness, and species diversity (Shannon's diversity index) – were all highest along mature forest / clearcut edges and lowest along young forest / clearcut edges (Table 7). Mean total bird abundance varied from 4.00 to 11.25 individuals per plot; species richness varied from 2.83 to 7.52 species per plot; and species diversity varied from 1.18 to 2.53 per plot. Variation in bird abundance and species richness was lowest along mature forest / clearcut edges and highest in mature forest habitat. Shannon diversity was also least variable along mature forest / clearcut edges, but it was most variable along young forest / clearcut edges.

Table 7: Mean and standard deviation of three bird community variables averaged over 4 sampling dates. Community variables are based on 69 bird species. Bold figures indicate highest values for each variable. See Table 3.4 for definitions of abbreviations.

Bird community variable	Clearcut (n=15)	Young forest (n=27)	Mature forest (n=60)	Young/cut edge (n=3)	Mat/cut edge (n=12)
TOTN	6.58 ± 2.20	5.33 ± 2.46	9.02 ± 2.60	4.00 ± 2.24	**11.25 ± 1.32**
NSPP	3.60 ± 1.52	3.96 ± 1.47	6.18 ± 1.60	2.83 ± 1.53	**7.52 ± 0.29**
SHDI	1.28 ± 0.56	1.58 ± 0.42	2.20 ± 0.37	1.18 ± 0.58	**2.53 ± 0.28**

Of the 69 bird species detected in the Beaverfoot study area in 1993, 25 species were present in ≥ 7 plots (Table 8). Eleven species were most commonly detected in plots located in mature forest habitat (Townsend's Warbler, Swainson's Thrush, Golden-crowned Kinglet, Varied Thrush, Brown Creeper, Boreal Chickadee, Mountain Chickadee, Hairy Woodpecker, and Winter

Wren, Spruce Grouse). The three most abundant of those species, Townsend's Warbler, Swainson's Thrush and Golden-crowned Kinglet, were also commonly found along mature forest / clearcut edges. Three bird species were most abundant in young forest habitat type: Yellow-rumped Warbler, Black-capped Chickadee, and Solitary Vireo. Yellow-rumped Warbler was also relatively abundant in the other habitat and edge types. Only two species, Chipping Sparrow and Vesper's Sparrow, showed a preference for clearcut habitat. Of these two species, Chipping Sparrow was also commonly found along mature forest / clearcut edges.

Table 8: Average abundance per plot and standard deviation (over 3-4 sampling dates) of bird species observed in clearcuts, young forests, mature forests, and along forest/clearcut edges. Bold figures highlight the habitat or edge type in which each bird species was most abundant. Bird species codes are described in Appendix 3.

Bird Species	No. plots present	Total obs.	Clearcut (n=15)	Young forest (n=27)	Mature forest (n=60)	Young/cut edge (n=3)	Mat/cut edge (n=12)
CHSP	53	67.50	**1.63 ± 0.79**	0.32 ± 0.37	0.38 ± 0.57	-	0.96 ± 0.40
VESP	9	10.50	**0.37 ± 0.67**	-	0.04 ± 0.14	-	0.23 ± 0.38
YRWA	74	71.00	0.25 ± 0.31	**1.03 ± 0.69**	0.48 ± 0.44	0.50 ± 0.00	0.75 ± 0.21
BCCH	18	17.00	-	**0.27 ± 0.40**	0.15 ± 0.28	-	0.08 ± 0.12
SOVI	22	9.25	-	**0.22 ± 0.32**	0.05 ± 0.13	-	-
TOWA	68	97.50	0.02 ± 0.06	0.24 ± 0.33	**1.35 ± 0.89**	-	0.83 ± 0.73
SWTH	80	85.25	0.12 ± 0.27	0.56 ± 0.53	**0.95 ± 0.59**	0.50 ± 0.50	0.81 ± 0.36
GCKI*	63	62.50	-	0.31 ± 0.45	**0.80 ± 0.49**	-	0.50 ± 0.30
VATH	32	25.75	0.02 ± 0.06	0.17 ± 0.28	**0.32 ± 0.36**	0.17 ± 0.29	0.13 ± 0.25
BRCR*	16	13.25	-	-	**0.22 ± 0.29**	-	-
BOCH	20	16.25	-	0.12 ± 0.22	**0.20 ± 0.31**	-	0.08 ± 0.12
MOCH	24	11.50	-	0.03 ± 0.14	**0.16 ± 0.25**	-	0.08 ± 0.29
HAWO*	24	8.75	0.02 ± 0.06	-	**0.13 ± 0.22**	-	0.08 ± 0.16
WIWR*	12	5.25	-	-	**0.09 ± 0.22**	-	-
SPGR	22	7.50	0.05 ± 0.10	0.05 ± 0.10	**0.08 ± 0.19**	-	0.04 ± 0.10
AMRO	18	23.00	0.15 ± 0.23	0.10 ± 0.16	0.15 ± 0.24	**0.83 ± 1.44**	0.56 ± 0.57
PISI	22	8.75	0.12 ± 0.23	0.07 ± 0.18	0.06 ± 0.20	**0.17 ± 0.29**	0.08 ± 0.12
GRJA	47	22.00	0.07 ± 0.20	0.12 ± 0.23	0.21 ± 0.30	**0.33 ± 0.58**	**0.33 ± 0.47**
DEJU	94	128.00	1.85 ± 1.06	0.70 ± 0.51	0.89 ± 0.88	1.00 ± 0.87	**2.08 ± 0.80**
RBNU*	49	47.00	-	0.08 ± 0.14	0.55 ± 0.40	0.17 ± 0.29	**0.92 ± 0.47**
RCKI	16	15.50	-	0.06 ± 0.14	0.13 ± 0.25	-	**0.50 ± 0.51**
OCWA	23	23.25	0.37 ± 0.46	0.20 ± 0.35	0.13 ± 0.38	-	**0.38 ± 0.45**
WAVI	16	6.25	0.05 ± 0.19	-	0.06 ± 0.12	-	**0.17 ± 0.37**
WIWA*	31	10.75	0.08 ± 0.15	0.03 ± 0.08	0.12 ± 0.21	-	**0.15 ± 0.20**
HAFL*	17	7.00	0.07 ± 0.20	0.06 ± 0.14	0.06 ± 0.17	-	**0.08 ± 0.16**

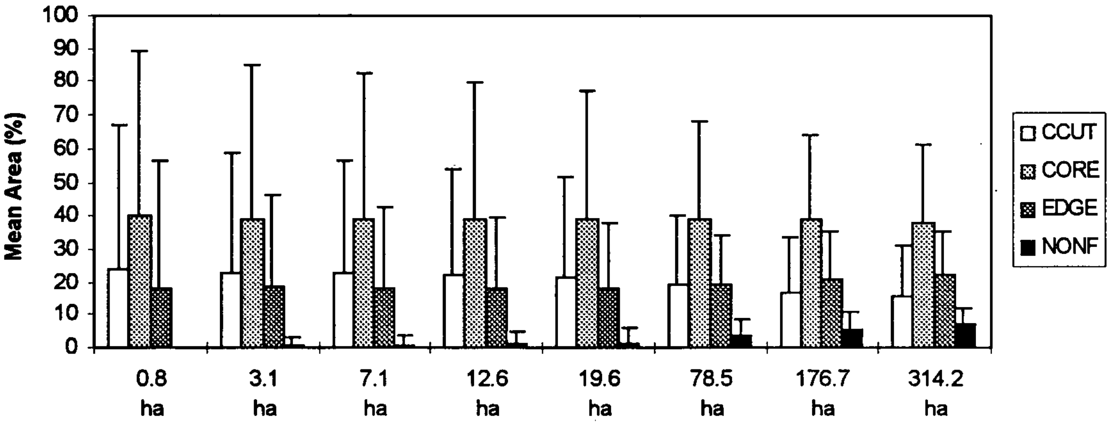
* Birds associated with late-successional and old growth forests (FEMAT 1993).

Ten bird species were most commonly detected along forest / clearcut edges. Seven of these species showed a preference for mature forest / clearcut edges while two species were most common along young forest / clearcut edges. Gray Jay was equally abundant in both types of edges. Finally, seven of the bird species occurred in all five habitat and edge types: Swainson's Thrush, Varied Thrush, Yellow-rumped Warbler, Dark-eyed Junco, Gray Jay, American Robin, and Pine Siskin.

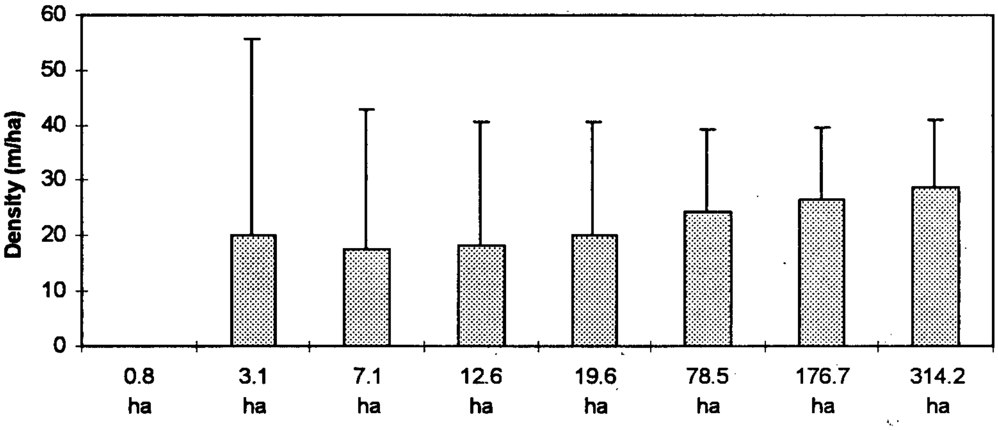
Neighbourhood Habitat Patterns

Several patterns emerge from the relations between landscape variables and the spatial extent of habitat neighbourhoods (Figure 11). Several variables were equal to zero for the 0.8 ha neighbourhoods (percent non-forest, high contrast edge density, and patch diversity). As circle size (i.e., habitat neighbourhood) increased, the percentage of mature forest edge habitat increased from 18% to 22% while the amount of clearcut habitat decreased from 24% to 16%. The percentage of core (mature forest interior) and young forest habitat was nearly constant for all of the concentric circles. Non-forest habitat increased in proportion from 1% of the 3.1 ha plots to 7% of the 314.2 ha plots. High contrast edge density was fairly constant between the 3.1 ha and 19.6 ha circles (varying around 20 m/ha) before increasing to 29 m/ha for the 314 ha habitat neighbourhood. Finally, patch evenness, as measured by Simpson's evenness index, increased predictably as circle size increased. The standard deviations for all variables except non-forest habitat decreased with increasing neighbourhood size reflecting a tendency for habitat patterns to become more similar to each other (and the landscape as a whole) as the spatial extent of the sampling unit increases.

(a) Percent Habitat Type as a Function of Circle Size



(b) Edge Density as a Function of Circle Size



(c) Simpson's Evenness as a Function of Circle Size

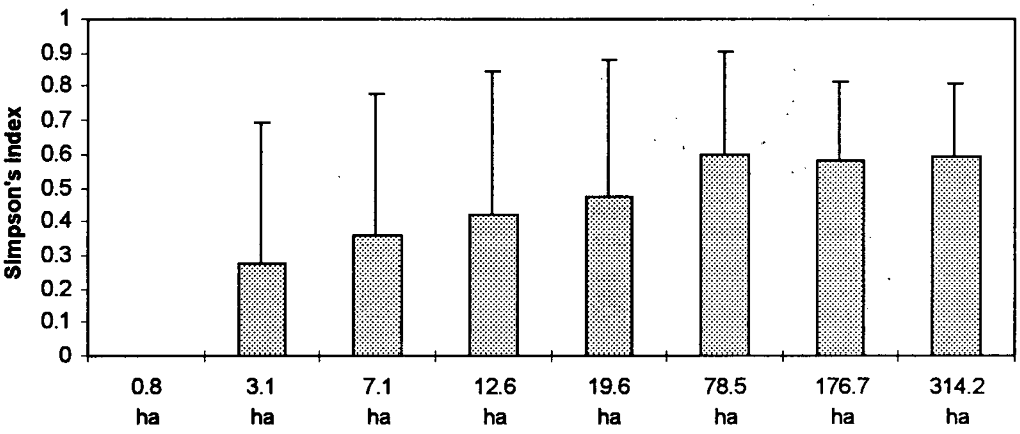


Figure 11: The effect of increasing circle size on percent habitat types (a), high contrast edge density (b), and patch evenness (Simpson's evenness index) (c).

Habitat-Habitat Correlations

The relations between habitat neighbourhood variables for the 19.6 ha circles was examined using a correlation matrix (Table 9). High contrast edge density and Simpson's evenness index had the highest significant correlation among the variables (r = 0.77). Both of these variables were also significantly correlated with percent clearcut, percent core habitat, and percent edge habitat. In each case, though, the relation was stronger with high contrast edge habitat than with Simpson's index. Core habitat was negatively correlated with clearcut habitat (r = - 0.62) and edge habitat (r = -0.39) while edge habitat was negatively correlated with young forest habitat (r = -0.48). Non-forest habitat, in contrast to the other variables, was not significantly correlated with any of the landscape variables.

Table 9: Correlation matrix of landscape variables for 19.6 ha circles. Values in bold type indicate a significant correlation at the p ≤ 0.05 level using Bonferroni-adjusted probabilities. See Table 3.4 for definitions of codes.

	CCUT	YOUN	CORE	EDGE	NONF	EDGE	SIEI
CCUT	1.00						
YOUN	-0.32	1.00					
CORE	**-0.62**	**-0.39**	1.00				
EDGE	0.30	**-0.48**	-0.33	1.00			
NONF	-0.23	0.06	-0.04	0.10	1.00		
EDGE	**0.62**	-0.18	**-0.66**	**0.63**	0.13	1.00	
SIEI	**0.45**	-0.08	**-0.56**	**0.53**	0.09	**0.77**	1.00

Bird-Habitat Correlations

The relations between the bird population and community variables and habitat neighbourhood variables for the 19.6 ha circles were also examined using a correlation matrix (Table 10). All three bird community variables (total bird abundance, species richness, Shannon diversity) were negatively correlated ($p \leq 0.05$) with young forest habitat and positively correlated ($p \leq 0.05$) with mature forest edge habitat.

Each bird population variable was significantly correlated ($p < 0.05$) with at least one habitat neighbourhood variable. Four birds (Dark-eyed Junco, Chipping Sparrow, Vesper's Sparrow, and Orange-crowned Warbler) were most strongly correlated with percent clearcut habitat. The former two birds were also positively correlated to high contrast edge density, patch evenness, and negatively associated with percent core habitat. Another group of four birds (Golden-crowned Kinglet, Brown Creeper, Townsend's Warbler, and Swainson's Thrush) were either positively associated with core habitat, negatively associated with clearcut habitat, or both. Finally, Red-breasted Nuthatch was positively associated with percent young forest while Yellow-rumped Warbler was negatively associated with the same habitat type. No bird species was significantly correlated with mature forest edge habitat or non-forest habitat.

Table 10: Correlation matrix of selected bird variables with landscape variables for 19.6 ha circles. Values in bold type indicate a significant correlation at the $p \leq 0.05$ level using Bonferroni-adjusted probabilities. See Table 3.4 and Appendix 3 for definitions of codes.

	CCUT	YOUN	CORE	EDGE	NONF	HCED	SIEI
TOTN	0.21	**-0.56**	0.06	**0.53**	-0.01	0.23	0.28
NSPP	0.08	**-0.53**	0.14	**0.54**	-0.03	0.19	0.30
SHDI	-0.06	**-0.55**	0.28	**0.48**	0.01	0.05	0.17
DEJU	**0.66**	**-0.20**	**-0.44**	0.25	-0.17	**0.36**	**0.37**
CHSP	**0.62**	-0.08	**-0.48**	0.14	-0.05	**0.50**	**0.44**
VESP	**0.50**	-0.18	-0.27	0.09	-0.09	0.14	0.11
OCWA	**0.35**	-0.12	-0.24	0.16	-0.09	0.20	**0.33**
GCKI	**-0.37**	**-0.41**	**0.55**	0.15	0.18	-0.20	-0.20
BRCR	-0.30	-0.28	**0.47**	0.01	0.09	-0.26	**-0.37**
TOWA	**-0.33**	**-0.39**	**0.46**	0.25	0.12	-0.17	-0.14
SWTH	**-0.34**	-0.18	0.32	0.19	-0.01	-0.18	-0.17
YRWA	-0.09	**0.38**	-0.33	0.14	0.03	0.08	0.16
RBNU	-0.05	**-0.39**	0.22	0.33	-0.09	0.05	0.05

4.3.2 Multiple Regression Analysis

Habitat Regression Models

Statistically significant habitat regression models were successfully developed for 22 of the 25 bird species sampled in ≥ 7 plots (Appendix 4). Only habitat models for which landscape (habitat pattern) variables explained greater than 18% of the variation in bird abundance are discussed (Table 11). All three community variables were most strongly related to the proportion of mature forest edge habitat present in the surrounding habitat neighbourhood. The proportion of young forest and mature forest edge habitat explained 43% of the variation in total bird abundance (TOTN) inside the 7.1 ha habitat neighbourhood. Five variables, within the 12.6 ha habitat neighbourhoods, explained 49% and 51% of the variation in species richness (NSPP) and species (Shannon) diversity (SHDI), respectively. Core habitat, edge habitat, high contrast edge density, and patch evenness (Simpson's evenness index) were common predictors for species richness and species diversity.

Among 8 of the 10 bird species for which landscape variables explained > 18% of the variation in abundance, the regression analysis suggested two habitat use/pattern groups: early-seral forest and late-seral forest. Two species (Yellow-rumped Warbler and Red-breasted Nuthatch) could not be placed in either of the two groups. The early-seral forest group included Chipping Sparrow, Dark-eyed Junco, Vesper's Sparrow, and Orange-crowned Warbler. Landscape variables explained 49%, 49%, 30%, and 25%, respectively, of the variation in the abundance of those 4 species. Percent clearcut habitat was the most important variable for all 4 species. Patch evenness was also important for 3 of the 4 bird species (excluding Vesper's Sparrow) while negative high contrast edge density was important for another three birds (excluding Chipping Sparrow). Percent edge habitat was also included in the Dark-eyed Junco habitat model.

The late-seral forest group consisted of Golden-crowned Kinglet, Townsend's Warbler, Brown Creeper, and Swainson's Thrush. Landscape variables explained 47%, 40%, 30%, 25%, respectively, of the variation in the abundance of those 4 species. Percent core and edge habitat were included in all 4 habitat models. Core habitat was the most important variable for 3 of the species (excluding Swainson's Thrush) while percent edge habitat was the most important variable for Swainson's Thrush. Percent non-forest habitat was also included in the Golden-crowned Kinglet habitat model; negative patch evenness in the Brown Creeper model; and negative percent clearcut habitat in Swainson's Thrush model.

Of the two species which were not placed in one of the two habitat use/pattern groups, Yellow-rumped Warbler's abundance was best predicted by young forest (most important) and mature forest edge habitat while Red-breasted Nuthatch abundance was negatively related to the amount of young forest (most important) and clearcut habitat. Habitat pattern variables explained 27% of the variation in abundance in both models.

Table 11: Habitat models generated by stepwise regression analysis. Only variables significant at $p \leq 0.05$ are included; n=117. Shaded cells indicate the variable which had the highest partial correlation for each model. Regression diagnostics* (Diagn) are shown in last column (ok = no problems; non = non-normality). Codes are defined in Table 3.4 and Appendix 3.

Bird	Circle			Landscape variables						Model	
variable	(ha)	CCUT	YOUN	CORE	EDGE	NONF	HCED	SIEI	R^2	SEy	Diagn
TOTN	7.1		-		**+**				0.43	2.37	ok
NSPP	12.6	+		+	**+**		-	+	0.49	1.48	ok
SHDI	12.6		-	+	**+**		-	+	0.51	0.44	ok
CHSP	7.1	**+**						+	0.49	0.50	non
DEJU	12.6	**+**			+		-	+	0.49	0.69	non
VESP	19.6	**+**					-		0.30	0.26	non
OCWA	12.6	**+**					-	+	0.25	0.35	non
YRWA	19.6		**+**		+				0.27	0.46	non
RBNU	3.1	-	**-**				+		0.27	0.38	non
GCKI	12.6			**+**	+	+			0.47	0.38	ok
TOWA	19.6			**+**	+				0.40	0.70	non
BRCR	19.6			**+**	+			-	0.30	0.20	non
SWTH	19.6	-		+	**+**				0.25	0.52	ok

* K-square test for non-normality, Q test for autocorrelation, and Sztroeter's test for heteroskedasticity were performed in that order.

Effects of Habitat Classification

The use of a more extensive classification system with 8 patch types (Table 1) did not affect the results of the stepwise multiple regression analysis for the bird community variables for the 19.6 ha circles. Among the bird population regression models, only the Swainson's Thrush habitat model was improved by the use of the more extensive classification system ($R^2 = 0.31$ for the expanded classification model vs. 0.25 for the original model).

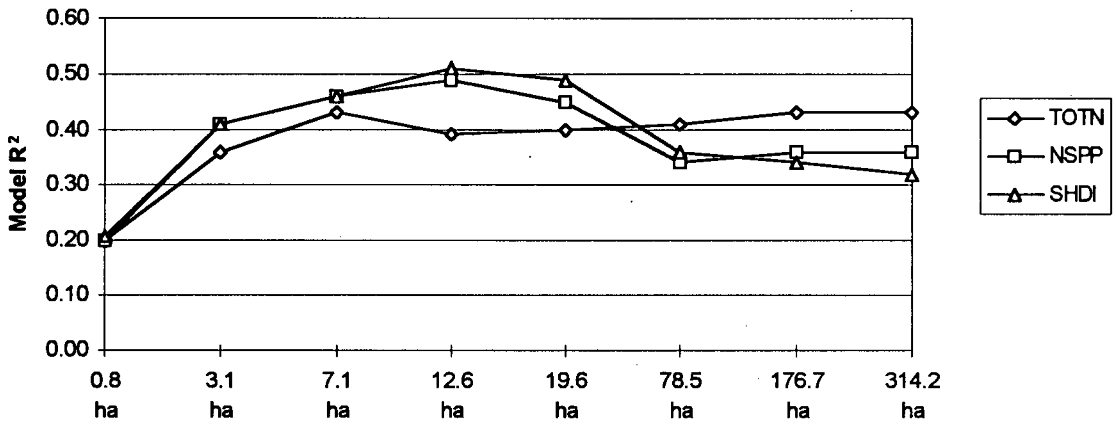
Effects of Spatial Extent of Neighbourhood

The proportion of the variation in bird diversity and abundance explained by the landscape variables was generally highest for the 12.6 ha and 19.6 ha habitat neighbourhoods (Table 12, Figure 12). There were three exceptions. Chipping Sparrow and Red-breasted Nuthatch habitat models were strongest for the 7.1 ha and 3.1 ha circles (habitat neighbourhoods), respectively. The total bird abundance habitat model (TOTN) was unique in that it was equally strong for the 12.6, 176.7, and 314.2 ha circles. The strength of the habitat models varied much less with circle size for the bird community models as well as for the Dark-eyed Junco and the Golden-crowned Kinglet than for the other bird population models (Figure 12). The model R^2 for many of the habitat models appear to drop off sharply after 19.6 ha. This is in part due to an increase in the interval between the circles after 19.6 ha (i.e., from 50 m radius interval to 250 m radius interval). The standard error of the estimate (SEy) was negatively correlated with R^2 (not shown in Table).

Table 12: Effects of spatial extent on R^2 for TOTN, NSPP, SHDI, and selected bird species. Dark grey cells have the highest and light grey cell the second highest model R^2 for a particular bird variable. Codes are defined in Table 3.4 and Appendix 3.

Bird	0.8 ha	3.1 ha	7.1 ha	12.6 ha	19.6 ha	78.5 ha	176.7 ha	314.2 ha
TOTN	0.20	0.36	0.43	0.39	0.40	0.41	0.43	0.43
NSPP	0.20	0.41	0.46	0.49	0.45	0.34	0.36	0.36
SHDI	0.21	0.41	0.46	0.51	0.49	0.36	0.34	0.32
CHSP	0.41	0.48	0.49	0.48	0.45	0.25	0.18	0.18
DEJU	0.31	0.42	0.43	0.49	0.43	0.36	0.30	0.32
GCKI	0.34	0.43	0.45	0.47	0.46	0.40	0.36	0.31
TOWA	0.28	0.35	0.38	0.39	0.40	0.27	0.20	0.13
BRCR	0.19	0.22	0.23	0.23	0.30	0.27	0.15	0.19
VESP	0.23	0.22	0.23	0.24	0.30	0.24	0.12	0.09
YRWA	0.17	0.21	0.24	0.26	0.27	0.19	0.19	0.20
RBNU	0.06	0.27	0.25	0.23	0.22	0.18	0.20	0.21
SWTH	0.16	0.19	0.21	0.23	0.25	0.23	0.16	0.16
OCWA	0.13	0.19	0.18	0.25	0.22	0.14	0.07	0.12

(a) Effect of Circle Size on Strength of Bird Community Models



(b) Effect of Circle Size on Strength of Bird Population Models

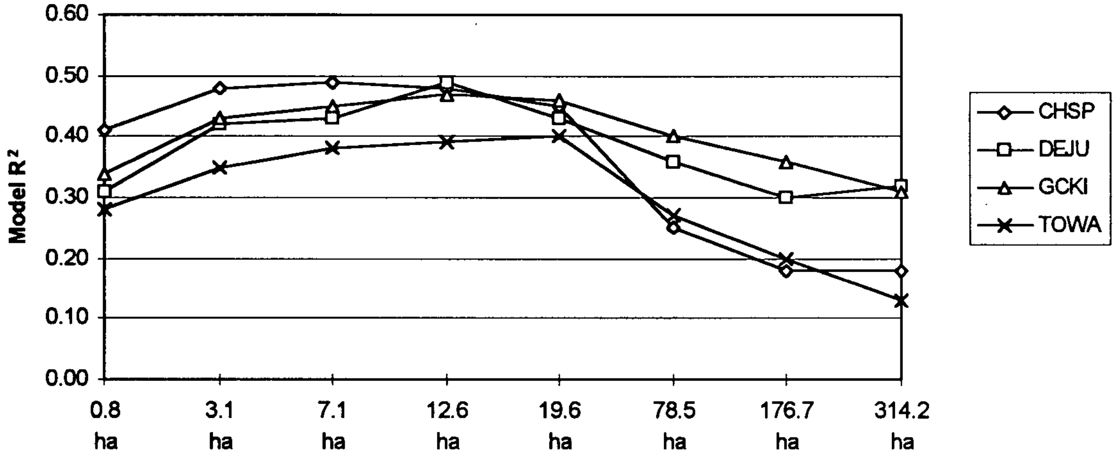


Figure 12: Effect of circle size on the strength (model R^2) of bird community regression models (a) and selected bird population regression models (b).

5.0 Discussion

5.1 Spatial and Temporal Changes in Landscape Patterns

5.1.1 Landscape Structure and Disturbance Patterns

This study has compared the structure of a managed montane spruce landscape to (1) conditions in adjacent protected montane spruce landscapes and to (2) historical conditions within the same landscape. The spatial and temporal patterns that were described appear to be related to variations in natural disturbances and human activities. Local variation in topography and soils (topoedaphic factors) was controlled by limiting the analysis to the dry cool montane spruce (MSdk) biogeoclimatic subzone (Meidinger and Pojar 1991). Historically, wildfire was probably the most important large-scale natural disturbance type in the region until fire suppression policies were initiated in the early part of the twentieth century (Achuff *et al.* 1984). A fire history analysis of the Rocky Mountain parks estimated the fire cycle (mean fire return interval) for Kootenay National Park to be 110 years until approximately 65 years ago (Van Wagner 1995). The last large wildfire in the montane spruce study area occurred in 1926.

In the past 40 years, clearcut logging has replaced wildfire as the dominant disturbance process in the managed montane spruce landscape. Current managed landscape patterns are the result of historical wildfire patterns (older than 65 years) and current harvesting patterns (less than 40 years old). In contrast, current protected landscape patterns are mainly related to historical wildfire patterns (older than 65 years). The historical managed landscapes represented variations in the areal extent of human activities. The four current and five historical landscapes that were analysed in this study represent different combinations of natural disturbances and human activities (Figure 4, Figure 7). The protected YNP landscape was unaffected by any large scale disturbances (natural or human) in the past 80 years and consisted of a few non-forest patches (mainly wetlands and lakes) embedded within a well connected, contiguous late-seral forest matrix. The other protected landscape, KNP, was affected by the 1926 wildfire and consisted of a mosaic of mid- and late-seral forest patches. The two managed landscapes have been extensively logged since 1953 but only the SEBF was affected by the 1926 wildfire. The NWBF landscape comprised numerous clearcuts and a few non-forest and mid-seral forest patches embedded within a late-seral forest matrix. The SEBF landscape was the most complex landscape, consisting of clearcuts embedded in two different matrices: a mid-seral matrix (approximately 67 years old in 1993) and a late-seral forest matrix. The historical managed landscapes (NWBF + SEBF) represented a gradient of human activities. The 1953 landscape consisted of a large, contiguous late-seral forest matrix and a smaller, contiguous mid-seral forest matrix. As logging progressed, clearcuts increasingly fragmented the late seral forest matrix and to a lesser extent the mid-seral forest matrix. The 1993 landscape was a combination of the NWBF and SEBF landscapes described above.

5.1.2 Effects of Logging on Landscape Structure

The purpose of quantifying managed, protected, and historical landscapes was to determine the effects of clearcutting on the composition and configuration of habitat patches in the montane spruce zone. Measurable differences between managed and protected landscapes as well as between managed and historical landscapes could be taken as evidence of the effects of clearcut logging. An understanding of protected and historical landscape patterns can provide guidance in designing management plans which more closely mimic natural patterns of habitat distribution and abundance across large areas. Several structural differences, attributable to clearcutting, distinguished the managed montane spruce landscape from historical conditions and adjacent protected landscapes. Other differences were interpreted in relation to natural disturbances or a combination of logging and natural disturbances. The direction of landscape change, as measured by indices of landscape structure, was fairly predictable. The degree of change in each landscape characteristic, though, was less predictable.

Effects on Seral Stage Patterns

Clearcutting in the montane spruce zone has clearly altered the number and proportion of early-, mid-, and late-seral forest patches through the process of habitat fragmentation. One of the most distinguishing characteristics between managed and protected landscapes was the absence of early-seral forest patches (0-25 years) in the protected landscapes. Conversely, in the managed landscapes, early-seral forest patches comprised between 18% and 29% of the area. All of the early-seral forest patches were generated by timber harvesting. In fact, natural early-seral forest patches were not present anywhere within the MSdk subzone of the study area. Mid-seral forest patches (25-80 years) were common only in the KNP and SEBF landscape units, where the 1926 wildfire occurred. Late-seral forest habitat was a major component in all landscapes (> 50% of each landscape), especially in the YNP landscape where it occupied 88% of the landscape. The other two landscapes had similar patterns for those three indices.

The temporal pattern analysis revealed similar trends in seral stage patterns. The number of early-, mid-, and late-seral forest patches all increased with time. The number of early-seral patches progressively increased as a direct result of logging. Mid- and late-seral patches were created by the fragmentation of the matrix as well as larger patches into smaller and more numerous patches. The proportion of the landscape in clearcut habitat also increased steadily at the expense of late-seral and, to a lesser extent, mid-seral forest habitat. The largest mid- and late-seral patches both decreased in size over time, also as a consequence of the break up of the matrix and larger patches. Changes in seral stage patterns were most pronounced in the last 5 year interval (between 1988 and 1993) when clearcutting increased in intensity and areal extent.

The spatial and temporal changes in seral stage patterns were both predictable (common sense) and observed in two similar studies. In a study comparing managed and unmanaged landscape patterns, old growth forest comprised a greater proportion of a natural landscape (74%) than an adjacent managed landscape (18%) in northern Wisconsin (Mladenoff *et al.* 1993). The managed landscape was dominated by second growth forest (58%). In another study analysing historical changes in landscape conditions in the Olympic National Forest, Washington, the amount of old growth forest was found to be reduced by 76% between 1940 and 1988 (Morrison 1990). In 1940, more than 42% of old forest habitat was found in one contiguous patch while in 1988 the total amount of old forest was reduced to less than 50% of that one patch.

Effects on Core Area and Edge Density

Another clear impact of logging is the reduction of mature forest interior habitat (core area) and the creation of high contrast forest/clearcut edges through edge effects, a direct consequence of habitat fragmentation. Core area made up a much greater proportion of the protected landscapes, even when late-seral forests comprised a smaller proportion of the landscape. For example, the KNP landscape unit, which contained less late-seral forest than the NWBF landscape, had almost twice the amount of core habitat as the NWBF landscape. The largest core area index was also much greater in the protected landscapes. The proportion of edge habitat was inversely related to core habitat (i.e., the managed landscapes contained a greater amount of edge habitat than the protected landscapes). Mean core area and core area standard deviation were also greater in the two protected landscapes than in the managed landscapes. Finally, the density of high contrast edges in the managed landscapes was approximately twice the density in protected landscapes.

Historically, the effects of clearcutting resulted in the progressive break up and isolation of mature forest interior habitat. As the proportion of the landscape in clearcuts increased over time, the number of core areas increased while the proportion of the landscape in core habitat decreased. Although the number of late-seral forest patches increased moderately from 15 to 23, the number of core areas increased more than fivefold (from 33 to 168). These results, of course, are dependent on the investigators definition of core habitat. During the same time period, the density of high contrast forest/clearcut edges more than doubled. The inclusion of roads, and thus edge effects due to roads, in the analysis would have amplified the differences by creating more edge habitat and reducing the proportion of core habitat.

Two recent forest fragmentation studies have found similar patterns. In the Willamette Natural Forest, Oregon, the amount of forest-to-clearcut edge doubled between 1972 and 1987 (Ripple *et al.* 1991). At the same time, interior habitat (100-metre edge effect) was reduced by 18% and the average interior patch size also decreased by 17%. Moreover, total forest patch edge almost doubled in the same time period. In the Olympic National Forest study, 41% of the remaining old growth in 1988 was within 170 m of an edge.

Effects on Patch Size and Shape

Clearcutting resulted in changes in the size and shape of all seral patch types through the fragmentation of mature forest and, to a lesser extent, of young forest habitat. Clearcuts, which only occurred in the managed landscapes, were smaller in size, but more variable (higher coefficient of variation), in the SEBF landscape than in the NWBF landscape. This phenomenon was due to the smaller size of the clearcuts in the young forest matrix (Figure 4). Mid-seral forest mainly occurred in the two southeastern landscapes. Young forest patches were more numerous, smaller on average, and less variable in the KNP landscape than in the SEBF landscape. Late-seral forest, common in all four landscapes, consisted of much larger patches in the YNP landscape than in the other landscapes. This is not surprising because one patch made up 88% of the landscape. The other three landscapes, which had more patches than YNP, did not reveal any clear effects of logging. Late-seral patches in the KNP landscape were intermediate in size and variability to the two managed landscapes. In all cases, patch size standard deviation was greater than mean patch size, indicating a non-normal patch size distribution. Patch shapes, measured by their fractal dimension, in the protected landscapes were marginally more complex than in the managed landscapes.

The effects of logging on patch size and shape were more clear from the analysis of historical landscape patterns. For example, the average size of mid- and late-seral patches was reduced by more than half over the past 40 years. The greatest change occurred between 1988 and 1993. Patch size variability also decreased over time as the number of patches of all forest types increased. The effect of clearcutting on patch shape, as measured by fractal dimension, was most evident for the landscape as a whole and for early- and late-seral forest patches. Patch shape complexity for all patches in the landscape decreased over time due to the addition of simple-shaped (rectangular) clearcuts. Not surprisingly, the shape of clearcuts were much simpler than that of other patch types. Moreover, clearcut fractal dimension remained constant over time, indicating that the shape of clearcuts in 1953 were similar to those in 1993. In contrast to the increasing simplification of patch shape for all patch types taken together, the fractal dimension of late-seral patches increased over time. This is the result of the perforation and fragmentation of the late-seral forest matrix into smaller and more numerous patches. A matrix punctured by several clearcuts has a more complex shape than one that is homogeneous throughout.

A recent study which compared the spatial structure of a managed and a natural landscape also found similar patterns (Mladenoff *et al.* 1993). The managed landscape contained many more small forest patches and fewer large, matrix patches than the natural landscape. Moreover, the shape of patches (also measured using fractal dimension), were simpler than in the unmanaged landscape. This is similar to the finding in this study that overall patch shape in the landscape decreased over time. Similar patterns were also reported in a historical analysis of landscape conditions in the Olympic National Forest (Morrison 1990). Mean patch size and total area of old forests (> 200 years) decreased dramatically between 1940 and 1988. Whereas in 1940 most of the old growth was found in patches greater than 4000 ha, in 1988 only one old growth patch larger then 4000 ha remained (Morrison 1990).

Effects on Landscape Heterogeneity

Indices of heterogeneity were used to quantify aspects of the landscape as a whole such as patch density, patch diversity, and landscape contagion. The number of patches and patch density, two related indices, were highest in the managed landscapes in comparison to the protected landscapes. This was a direct effect of the addition of clearcuts and the break up of mid- and late-seral forest habitat. As expected, patch diversity was highest in the SEBF landscape, which was both logged and affected by the 1926 fire, and lowest in the YNP landscape, which was unaffected by recent disturbances. Interestingly, patch diversity was similar in the managed landscape which was logged but not burned (NWBF) and the protected landscape which was burned but not logged (KNP). Contagion, which reflects the amount of aggregation of patches of all types, was used to measure the spatial arrangement of patches. Contagion was related to the number of patches and patch types as well as their spatial arrangement. Contagion followed a similar, but inverse, pattern to patch diversity. It was highest in the least disturbed, and most contiguous landscape (YNP) and lowest in the most altered and diverse landscape. Like patch diversity, contagion was similar for the two moderately disturbed landscapes, being a little higher in the NWBF landscape than in the KNP landscape.

Over time, the total number of patches increased, mainly due to the increase in the number of clearcut patches. Patch diversity also increased due to the decreasing dominance of late-seral forest habitat and the increasing number of early-seral patches. Some landscape heterogeneity indices, such as patch richness and non-forest patch type metrics, did not vary because they were designed to remain constant over time. Finally, contagion decreased steadily over time, reflecting the loss and fragmentation of the contiguous late-seral forest matrix and a concomitant increase in the number and areal extent of other patch types, clearcuts in particular.

The results are consistent with results obtained by Mladenoff *et al.* (1993) which showed that patch diversity was higher in a disturbed (managed) landscape than in an undisturbed (old growth) landscape in northern Wisconsin. Contagion was not measured in any of the empirical studies that were reviewed. This measure, though, has been used by several authors involved in simulation studies (O'Neill *et al.* 1988, Li and Reynolds 1993, Riitters *et al.* 1995).

5.2 Bird Responses to Surrounding Habitat Pattern

5.2.1 Habitat Neighbourhoods and Landscape Variables

The hypothesized relation between landscape structure and bird species diversity and abundance is based on recent theoretical and empirical studies (Wiens 1989a, Lemkhul *et al.* 1991, Dunning *et al.* 1992, Pearson 1993, Wiens *et al.* 1993, McGarigal and McComb 1995). In this study, the influence of landscape structure on forest birds was evaluated by regressing bird response variables on landscape structure variables measured in concentric circles around bird point count locations. Concentric circles ranging from 0.8 ha to 314.2 ha were used to determine the effect of varying the spatial extent of habitat neighbourhoods on bird responses. The size of the smallest concentric circle (0.8 ha) was limited by the pixel size used in IDRISI whereas the largest circle was designed to encompass the home range size of the species with the largest home range (i.e., Pileated Woodpecker: 150-300 ha/pair). In a similar study on the relations between landscape structure and bird communities, habitat patterns were quantified around five separate 100 metre radius bands around each study plot (Pearson 1993). In another study focusing on the influence of surrounding habitat pattern on Northern Spotted Owl, circular areas which approximated the mean annual home range of owl pairs were used (Lemkhul and Raphael 1993).

The landscape variables selected for developing the bird-habitat pattern models reflected seral stage patterns (percent of landscape in each seral stage and non-forest type), edge effects due to clearcuts (percent core and edge habitat, high contrast edge density), and landscape heterogeneity (patch evenness). These variables (1) were assumed to be important habitat attributes for a wide variety of bird species in the Pacific Northwest (Thomas 1979, Brown 1985, Ritcey *et al.* 1988), (2) are commonly available from existing resource inventory data, and (3) are relatively easy to incorporate into forest management plans and landscape-level biodiversity monitoring programs (Stoms and Estes 1993).

5.2.2 Community Responses

Habitat pattern models accounted for 43% to 51% of the variation in species richness, species diversity, and total bird abundance. Mature forest edge habitat (i.e., mature forest habitat within 150 m of a clearcut or non-forest patch boundary) was the most important predictor for all three community variables. This was probably related to the relatively high within-patch structural diversity characteristic of forest edge habitat located along the boundary of clearcuts. Edge habitat was also in close proximity to core habitat and clearcut habitat. Thus birds associated with edge habitat could have been interior specialists, edge specialists, or generalists. The total number of bird species was also negatively related to the amount of young forest habitat. Young forests, typically, are very homogeneous and contain little within-patch heterogeneity. Species richness and diversity were also positively related to core area (mature forest interior habitat) and patch evenness (Simpson's evenness index) and negatively related to the density of high contrast edge.

Similar results were obtained in a study examining the influence of landscape-level factors on wintering bird populations in the piedmont region of Georgia, USA (Pearson 1993). Landscape factors (linear combinations of landscape variables) accounted for 74% and 82% of the variation in bird species richness and Shannon diversity respectively. The most important factors were related to the proportion of habitat types surrounding plot locations. The relatively high R^2 values may have been related to the use of a greater number of habitat types and landscape variables and to the larger scale aerial photographs used to create the habitat maps. Thus, although similar general patterns were found, the different scales used in both analyses prevents any substantive comparisons or generalizations. The relation between bird species richness located in Douglas-fir stands and landscape variables was also analysed in the Southern Washington Cascade Range (Lemkhul *et al.* 1991). Richness was found to be strongly influenced by the proportion of clearcut or late-seral forest within a stand's neighbourhood and within 2025 ha landscapes.

5.2.3 Species Responses

Bird species varied dramatically in their response to surrounding habitat patterns. Landscape variables accounted for 25% to 49% of the variation in the abundance of ten bird species. Regression analysis was also significant ($P \leq 0.05$) for twelve other species, but with low explained variation ($R^2 \leq 0.18$). The other three species, Pine Siskin, Spruce Grouse, and Warbling Vireo, were not significantly associated with any landscape variable. Possible reasons for the poor relationships between the latter 15 bird species and landscape variables may be related to the scale of the study (inappropriate grain and extent) and are discussed at the end of the chapter. Eight of the ten bird species which were moderately associated with surrounding habitat patterns, were classified into one of two groups: early-seral forest species (Chipping Sparrow, Dark-eyed Junco, Vesper's Sparrow, and Orange-crowned Warbler) and late-seral forest species (Golden-crowned Kinglet, Townsend's Warbler, Brown Creeper, and Swainson's Thrush). The other two species, Yellow-rumped Warbler and Red-breasted Nuthatch, are discussed on their own. The relations between bird species and surrounding habitat pattern were generally consistent with other studies and could be interpreted on the basis of each species' known habitat preferences at the stand level (Brown 1985, Galindo-Leal and Bunnell 1994).

The proportion of clearcut habitat surrounding bird locations was the strongest predictor for all four early-seral forest species. Edge habitat, high contrast edge density, and patch evenness, were also included in some of the regression models. The relations between the early-seral forest species and surrounding habitat patterns corresponded fairly well to each species known habitat preferences. Three of the four early-seral forest species, Chipping Sparrow, Dark-eyed Junco, and Orange-crowned Warbler, are considered to be forest-dwelling species associated with shrubs and grasses (Brown 1985). The former two species are also associated with some degree of canopy cover. The other early-seral forest species, Vesper's Sparrow, is also associated with shrubs, but is considered to be an open-habitat species (grassland and shrubland) (Galindo-Leal and Bunnell 1994).

Birds in the late-seral forest group were all associated with the proportion of core and edge habitat surrounding their locations. Core habitat was the most important predictor for three of the four species, the exception being Swainson's Thrush for which edge habitat was the strongest predictor. The late-seral species also corresponded well with broad habitat associations at the stand level. Golden-crowned Kinglet and Townsend's Warbler have both been associated with closed canopy conifer forests while Brown Creeper has been associated with structurally complex closed-canopy habitats as well as late-seral habitat attributes such snags and large trees (Brown 1985, Ehrlich *et al.* 1988, Hansen *et al.* 1995). Swainson's Thrush, meanwhile, has been associated with deciduous trees and shrubs and structurally simple closed-canopy forests (Ehrlich *et al.* 1988, Hansen *et al.* 1995). The late-seral forest patch type was broadly defined for the purpose of this study and consequently did not permit a distinction between various levels of within-patch structural complexity preferred by the late-seral species.

The habitat pattern associations for the two species not included in the early- or late-seral groups also corresponded well with known habitat preferences. Yellow-rumped Warbler, which has been correlated with closed-canopy conifer forests (Brown 1985), was associated with the proportion of young forest (strongest predictor) and edge habitat within its habitat neighbourhood. Red-breasted Nuthatch, which is associated with conifer forests and snags (Brown 1985), was negatively related to the proportion of clearcut and young forest (strongest predictor) habitat in its neighbourhood. This implied that this species is associated with mature forest core and edge habitat. This was checked by repeating the regression analysis without including clearcut and young forest variables. The strength of the relationship was almost identical, but this time Red-breasted Nuthatch was positively related to core and edge habitat, qualifying it for membership in the late-seral group.

Four recent studies have examined the influence of landscape structure on bird populations (Lemkhul *et al.* 1991, Lemkhul and Raphael 1993, Pearson 1993, McGarigal and McComb 1995). In the Cascade study described above, the authors found that some bird species were associated with stand neighbourhood (12.6 ha) and landscape (2025 ha) variables (Lemkhul and Raphael 1993). For example, Red-breasted Nuthatch was correlated with the proportion of clearcut habitat surrounding old growth stands. The apparent contradiction with the results obtained in the present study may be related to the packing of bird species, in that particular landscape, into remnant late-seral patches following harvesting (Whitcomb *et al.* 1981, Lemkhul *et al.* 1991). In another study, Pearson (1993) obtained similar results with landscape factors explaining up to 54% of the variation in individual bird models. In particular, the abundance of Dark-eyed Junco was in part explained by surrounding habitat richness and diversity.

In a third study, Lemkhul and Raphael (1993) analysed the influence of the habitat mosaic surrounding Northern Spotted Owl locations to assess the effects of habitat fragmentation on habitat selection and reproduction in the Olympic Peninsula of Washington. Percent owl habitat area (based on a map showing "typical" and "atypical" owl habitat) and variation in patch size accounted for 52% of the variation in habitat pattern. The fourth study analysed the relationship between landscape structure and the abundance of 15 bird species associated with late-seral forests in the Oregon Coast Range (McGarigal and McComb 1995). This study was unique because the authors systematically sampled throughout thirty 300 ha landscapes located in three different watersheds. Landscape structure (late-seral forest habitat area and configuration) accounted for up to 50% of the variation in species' abundances.

5.2.4 Effects of Spatial Extent

Habitat selection in birds has been hypothesized to occur at a variety of spatial scales, including the within-patch and landscape scales (Hutto 1985). For that reason, different bird species may be associated with different habitat factors at different scales (Hansen *et al.* 1993). In this study, the appropriate scale (spatial grain and extent) for developing the models was not known *a priori*. Consequently, the sensitivity of the bird-habitat models to one aspect of scale, spatial extent, was assessed. This was done by varying the spatial extent of the habitat neighbourhood (while keeping the spatial grain constant) and observing the effects on the strength of the regression models (R2) and the standard error of the estimate (SEy). The other aspect of scale, spatial grain, represented the lower limit of resolution of the study and was limited by the minimum mapping unit of the forest cover maps.

Habitat patterns within the 12.6 ha and 19.6 ha circles generally exerted a greater influence on individual bird species than did more proximal or distal patterns. For the community-level models, species richness and species diversity followed patterns which were similar to the species-level models. They were most influenced by 12.6 ha circles. The exception was the total abundance of birds which showed little variation among circles ranging from 7.1 ha to 314 ha. The reason that the smaller concentric circles (i.e., less than 12.6 ha) did not exert a greater influence may have been related to the scale of the analysis. Smaller concentric circles capture fewer patches at a given grain and may be more prone to small errors related to bird locations with respect to forest edges as depicted on the habitat patch maps. Medium sized circles may have better represented surrounding habitat patterns while larger circles may have reflected the decreasing importance of the neighbourhood's effect (Dunning *et al.* 1992).

The spatial extent of landscape influence on bird species has also been examined by Pearson (1993) who calculated the proportion of each of 10 habitat types for each of five 100 metre radius concentric circles surrounding each study plot. Habitat patterns within the first two 100-metre radius concentric circles were generally more influential than the more distant circles. Although the study designs were not identical, the results were similar (i.e., proximal habitat patterns generally seem to exert a greater influence on birds than more distal patterns). The influence of spatial extent was also assessed by Lemkhul and Raphael (1993) who measured habitat pattern attributes in concentric circles of 813 ha, 3253 ha, and 7320 ha around Northern Spotted Owl locations. The authors found that habitat patterns in the 3253 ha areas around owl locations were comparable to those found in owl home ranges (approximately 3,650 ha in Washington State).

5.3 Limitations of the Study

Several factors may have affected the results of the analysis. First, forest inventory data were not available for the entire montane spruce study area, so aerial photographs were used to map forest cover in the protected areas adjacent to the managed forests. In spite of using the same protocol that was used by MOF to map forest cover in the managed forests, differences in the stratification and identification of forest cover polygons probably contributed an unknown amount of variation to the results. This phenomenon is sometimes observed along map sheet edges due to inter-observer (aerial photo interpreter) differences (Goodchild *et al.* 1991). The positional and attribute accuracy of the data may also have contributed an unknown amount of variation to the results (Aronoff 1989).

Second, the spatial scale (i.e., grain and extent) defines the lower and upper limits of resolution of a study (Li and Reynolds 1993). Because spatial patterns and species' responses to those patterns may vary with scale, the grain and spatial extent of a study can limit a study's ability to describe spatio-temporal landscape patterns and to evaluate bird-habitat relationships (Wiens 1989a, McGarigal and McComb 1995). The spatial grain of this study was determined by the minimum mapping unit of the forest cover maps. These were set at 5 ha for forest stands and 2 ha for non-forest stands. Three different spatial extents were used depending on the analysis. The spatial extent of the landscapes used to compared managed and protected landscape patterns coincided with biogeoclimatic and management zone boundaries and ranged from 2387.5 ha to 7151.5 ha. The analysis of temporal changes in landscape patterns was limited to the managed montane spruce landscape which was 12118.8 ha in extent. The extent of the habitat neighbourhoods used to develop the bird-habitat models varied from 0.8 ha to 314.2 ha. The effects of changing the spatial extent on the habitat models was discussed in the previous section on bird responses to surrounding habitat patterns.

Third, the habitat classification system used in this study was developed from a bird community perspective. Habitat types were defined on the basis of seral stage (stand age) and crown closure, factors which are believed to be meaningful for a variety of bird species (Thomas 1979, Brown 1985, Galindo-Leal and Bunnell 1994). These types, though, may not necessarily be appropriate from an individual bird species' perspective. For example, some species may be more responsive to the density of large live trees and snags than to seral stage. Moreover, the classification system and spatial heterogeneity of the habitat patch maps were constrained by the information available on forest cover maps and the scale of the aerial photographs. Rare and important habitat types, such as riparian habitats, were not considered due to the limitations of forest cover maps at delineating such habitat types. The consequences of omitting rare habitat types on species diversity and abundance patterns is not known.

Fourth, the use of the two protected landscapes as models of natural landscape patterns should be considered within the context of past natural disturbance regimes. Neither protected landscape truly represented natural patterns because of fire control policies. Consequently, a more thorough understanding of natural landscape patterns will depend on detailed historical analyses of natural disturbance regimes (Masters 1989, Van Wagner 1995). Moreover, the landscapes used in this study are location specific. Caution should be used when applying the results to other locations, even within the montane spruce zone. It may be possible, though, to compare the results of several similar studies in different locations with a view towards extracting general characteristics which distinguish 'managed' and 'unmanaged' landscapes.

Fifth, edge effects due to roads were not considered because a complete network of roads was not available for the study area. Presumably, this would have increased the amount of forest edge habitat while reducing the proportion of forest interior habitat (Morrison *et al.* 1990). Sixth, the habitat models are limited to explaining the diversity and abundance of relatively common birds during the 1993 breeding season. Bird abundances may not have been typical due to natural stochastic variation, weather, and other factors (Bryant *et al.* 1993). Finally, rare and uncommon species were not considered because of the choice of statistical procedures used in this analysis. Other methods, such as logistic regression and discriminant analysis may have better described the relations between rare birds and landscape structure.

6.0 Conclusions and Management Implications

6.1 Conclusions

The majority of British Columbia's forests are being actively managed for timber and other resources while a smaller proportion has been set aside within a network of protected areas designed to protect biological diversity. In the past decade it has become clear that the long term maintenance of biological diversity and ecological processes will depend on the management of whole ecosystems and their components at large spatial and temporal scales. This new approach to resource management has been called ecosystem management (Galindo-Leal and Bunnell 1995). One of the keys to this approach, as well as the focus of this study, is a better understanding of the landscape-level interactions among human activities, natural disturbances, landscape patterns, and biological diversity.

Forest landscape patterns, whether 'managed' or 'unmanaged', are continually changing due to disturbance and successional processes. The spatial patterns created by human activities, though, vary dramatically from those created by natural disturbances. Historically, the mean disturbance return interval for the montane spruce biogeoclimatic zone was about 150 years. Stand replacing wildfires, and to a lesser extent, outbreaks of insects and diseases, were the most common large scale disturbance types. Past wildfires created landscapes that were characterized by mosaics of forest patches of different ages, sizes, and shapes. In the past 40 years, clearcutting has replaced wildfires as the dominant disturbance type in the montane spruce zone, altering historical patterns and processes, with consequences for wildlife and habitats that are poorly understood. Today, one of the key challenges in resource management is to understand and predict the effects of human activities in general and clearcutting in particular on wildlife and their habitats over large spatial and temporal scales. This study was designed to analyse the effects of clearcutting on birds and their habitats at the landscape level.

When managed landscape patterns were compared to conditions in adjacent protected landscapes and to historical conditions within the same landscape, a number of differences attributable to clearcutting were demonstrated. In particular, clearcutting has (1) increased the number of early-, mid-, and late-seral forest patches, (2) increased the total area of early-seral habitat at the expense of late-seral forest habitat and to a lesser extent of mid-seral forest habitat, (3) reduced the total area of mature interior forest habitat while increasing the number of core areas, (4) increased the total area of mature forest edge habitat, (5) increased the density of high contrast edges, (6) reduced mean patch size and variability of mid- and late-seral forest patches, (7) simplified the overall shape of patches in the landscape while increasing the complexity of late-seral forest patches, (8) increased patch diversity, and (9) reduced patch contagion.

When bird species diversity and abundance were analysed in relation to surrounding managed and protected landscape patterns, a number of moderate associations emerged. At the community level, bird species richness, diversity, and total abundance were found to be associated with the amount of surrounding mature forest edge habitat. At the population level, the relations between bird species abundance and surrounding landscape patterns were more varied. In particular, the abundances of Chipping Sparrow, Dark-eyed Junco, Vesper's Sparrow, and Orange-crowned Warbler were all positively associated with the proportion of clearcut habitat in the surrounding landscape. In contrast, the abundances of Red-breasted Nuthatch, Golden-crowned Kinglet, Townsend's Sparrow, Brown Creeper, and Swainson's Thrush were associated with the proportion of mature forest interior and edge habitat in the surrounding landscape. One species, Yellow-rumped Warbler, was associated with the proportion of surrounding young forest and edge habitat.

Other recent landscape-level habitat analyses have found that landscape patterns exert a similar moderate influence on bird species diversity and abundance (Lemkhul *et al.* 1991, Pearson 1993, McGarigal and McComb 1995). Whether the moderate influence of landscape patterns on birds observed in this study reflects reality or is related to the methodology used is unclear. Several factors may have impeded the observation of stronger associations, among them the scale of the study, the omission of important predictor variables, and the choice of statistical methods. One of these factors, the spatial extent of the surrounding landscape, was varied to determine its influence on the strength of the bird-habitat relations. In general, landscape patterns measured within 12.6 ha and 19.6 ha concentric circles were found to exert a greater influence on bird species diversity and abundance than smaller or larger circles.

Many more observational studies of this type will be necessary to improve our understanding of the interactions among landscape patterns, ecological processes, and human activities. These could be repeated using different locations, other wildlife species, and alternative methods. The main advantage of using already collected data, such as forest cover maps, is undeniably an economic one. However there are obvious and inherent limits to their usefulness. A more profound and comprehensive understanding of the complex interactions at work at the landscape level and their consequences for biological diversity will depend on more analytical investigations which rely on better quality data collected for this purpose. Critical to this approach would be the implementation of a monitoring strategy designed to track structural and functional indicators of biological diversity at the genetic, species, ecosystem, and landscape level (Noss 1990).

6.2 Management Implications

The successful implementation of ecosystem management in British Columbia's forest landscapes will depend in large part on the "rigorous combination of management, research, and monitoring so that credible information is gained and management activities can be modified by experience" (CSP 1995). This approach, referred to as adaptive management, can be used to conduct management experiments designed to test specific research hypotheses relating to the interactions among landscape structure, human activities, and ecological processes. Several implications for using an adaptive ecosystem management approach should be considered with respect to the maintenance of biological diversity at the landscape level.

Natural landscape patterns. Natural landscape patterns emerge from the dynamic interactions among topography, soils, disturbance, and successional processes. It is important for ecosystem managers to understand and emulate the structural patterns which characterized forest landscapes under historical natural disturbance regimes. Several landscape characteristics should be considered including: (1) the number, relative proportion, and diversity of forest types and seral stages, (2) the size and shape of forest patches, (3) the spatial and temporal distribution of forest patches including cutblocks, (3) the connectivity of late-seral forests and riparian corridors, (4) the proportion and connectivity of late-seral forest interior habitat, (5) the density and contrast of forest edges, and (6) the adjacency relationships between forest and non-forest patch types.

Natural disturbance and successional processes. Current forest practices emphasizing even-aged, even-sized, short rotation regimes need to emulate natural disturbance regimes with respect to variations in scale, frequency, and intensity. For example, in the montane spruce zone, wildfires historically ranged in size up to several thousand hectares, had a mean return interval of about 150 years, and were frequently stand replacing (but often leaving behind mature forest remnants, snags, and downed wood) (FPC 95). Current forest practices are also altering successional processes by shortening the time in early seral stages (grass-forb and shrub-seedling), emphasizing mid-seral stages, and eliminating late-seral and old growth stages.

Spatial scale and context. Because different species perceive their environment at different scales, a multi-scale approach will almost always be necessary (Wiens 1989a). Landscape and stand level habitat attributes are both important from a point of view of many species, especially those that have large home ranges, high dispersal capabilities, or require a wide variety of habitats (Morrison *et al.* 1992). Moreover, forest patches should not be managed in isolation from the landscape in which it is embedded. Similarly, landscapes should not be managed in isolation from the ecoregion in which it is embedded.

Information needs. Forest management in British Columbia has traditionally relied on the use of forest inventory data. There are three major problems with these data with respect to ecosystem management. First, the data are only collected within forest management boundaries. In other words, there is no consistency of information among different land management agencies. Second, the data have a timber management bias. They are collected for the management of timber and as such contain no information on understory vegetation, downed wood, snags, and other habitat attributes important for wildlife. Third, the resolution of the data is probably too coarse for the management of many birds and other wildlife species. The second issue is currently being addressed within the B.C. Ministry of Forests.

Interagency coordination. Ecosystem management, research, and monitoring must be conducted with the cooperation of all land and resource management agencies in a given region. This is necessary because of the large spatial and temporal scales involved in managing forest ecosystems and all of its elements. Moreover, the need for high quality data collected over long terms will necessitate a cooperative approach.

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Appendix 1. Forest Cover Error Assessment.

The forest cover maps were ground truthed in May 1994 to verify if the forest and non-forest polygons were correctly classified during the mapping process. The majority of the forest cover polygons in the MSdk subzone of both parks were visited in the field. Some of the polygons outside the MSdk subzone were also checked. Incorrectly interpreted polygons were updated. The following procedures was used to ground truth forest and non-forest types:

1. For each protected area, a path was selected to maximize the number of polygons visited in the MSdk subzone. All of the polygons which were near or along trails and fire roads were visited. Less accessible polygons were also visited when possible and if there was some doubt as to a particular polygon's identity.

2. For each polygon visited, a representative location was located at a minimum of 100 metres from a polygon boundary and at least 20 metres away from a trail of fire road. Random points were not selected because they might not be representative of a polygon. All selected locations were visited on foot using aerial photos and compass as navigation aids.

3. A visual assessment was made of each selected location as well as its surroundings. Notes were taken on the characteristics of each polygon and compared to the criteria discussed below. In cases where species composition or seral stage was not evident, a minimum of two 0.01 ha plots were established and overstory trees species composition and dbh were tabulated.

4. Field survey results were compared with the interpreted habitat maps and updated where necessary. The data collected for polygons which were not easily identified were compared to the criteria describe below to facilitate their identification. It was also possible to adjust some polygons which were not visited based on the new information acquired in the field.

The following characteristics were used to differentiate forest cover polygons on the basis of leading tree species:

Spruce/fir forest (SF): Any polygon where white spruce, Engelmann spruce, or subalpine fir is the leading or co-leading species. Other co-leading species or minor components may include lodgepole pine, Douglas-fir, and other conifer and deciduous species.

Lodgepole pine forest (Pl): Any polygon where lodgepole is the leading species. Spruce, fir, Douglas-fir, and deciduous species may be a minor component.

Douglas-fir forest (Df): Any polygon where Douglas-fir is the leading species or where lodgepole pine is a co-leading species. Spruce, fir, and poplar species may be a minor component.

Early-seral stages did not occur, probably due to fire suppression which has been in place for most of this century. Mid and late-seral stages were equally common in Kootenay National Park due to a widespread fire in 1926. Yoho was dominated by late-seral forests. The following characteristics were used to differentiate late-seral from mid-seral forests:

- evidence of thinning (dead understory trees)

- trees larger and more spaced than in mid-seral forests
- bark of overstory trees (dominant and co-dominant) is scaly, deeply furrowed, or thick
- presence of snags in the overstory
- presence of moderate to large amounts of coarse woody debris
- majority of overstory trees have dbh > 30cm
- understory regeneration of climax species (generally spruce/fir) well established
- thick carpet of moss present in moist forests

Results of the error assessment for Yoho and Kootenay National Parks are presented in the form of an error matrix (Figure 13). For Yoho National Park, 52% of the polygons (91% of the MSdk polygons) were ground-truthed with an accuracy of 95% (100% for the MSdk polygons). For Kootenay National Park, 41% of the polygons (57% of the MSdk polygons) were ground-truthed with an accuracy or 88% (88% for the MSdk polygons). Errors of omission represent cases where a particular category was found to be mapped as something different. Errors of commission represent cases where locations mapped as a particular category was found to be truly something else.

(a) YNP Error Matrix

Actual

Mapped		Lodgepole	Spruce/fir	Doug-fir	Wetland	Total	error %
	Lodgepole	3	0	0	0	3	0
	Spruce/fir	0	25	0	0	25	0
	Doug-fir	1	0	4	0	5	0.20
	Wetland	0	0	0	10	10	0
	Total	4	25	4	10	43	
	error %	0.25	0	0	0		0.05

errors of commission

errors of omission

(b) KNP Error Matrix

Actual

Mapped		Y-Pl	M-Pl	Y-SF	M-SF	M-Df	Shrb	Wtld	Lake	Rock	Rivr	Clear	Total	error %
	Y-Pl	23	0	0	0	0	0	0	0	0	0	0	23	0
	M-Pl	0	24	0	4	0	0	0	0	0	0	0	28	0.14
	Y-SF	0	0	3	0	0	0	0	0	0	0	0	3	0
	M-SF	0	1	0	15	0	0	0	0	0	0	0	16	0.06
	M-Df	0	0	0	0	1	0	0	0	0	0	0	1	0
	Shrb	0	0	0	0	0	4	4	0	0	0	0	8	0.50
	Wtld	0	0	0	0	0	2	9	1	0	0	0	12	0.25
	Lake	0	0	0	0	0	0	0	2	0	0	0	2	0
	Rock	0	0	0	0	0	0	0	0	1	0	0	1	0
	Rivr	0	0	0	0	0	0	0	0	0	3	0	3	0
	Clear	0	0	0	0	0	0	0	0	0	0	5	5	0
	Total	23	25	3	19	1	6	13	3	1	3	5	102	
	error %	0	0.04	0	0.21	0	0.33	0.31	0.33	0	0	0		0.12

errors of commission

errors of omission

Figure 13: Error matrix for Yoho National Park (a) and Kootenay National Park (b) forest cover polygons. Y= young; M= mature; Pl = lodgepole pine; SF = spruce/fir; Df = Douglas-fir; Shrb = shrubland; Wtld = wetland; Rivr = river; Clear = clearing.

Appendix 2. Map of Bird Point Count Locations

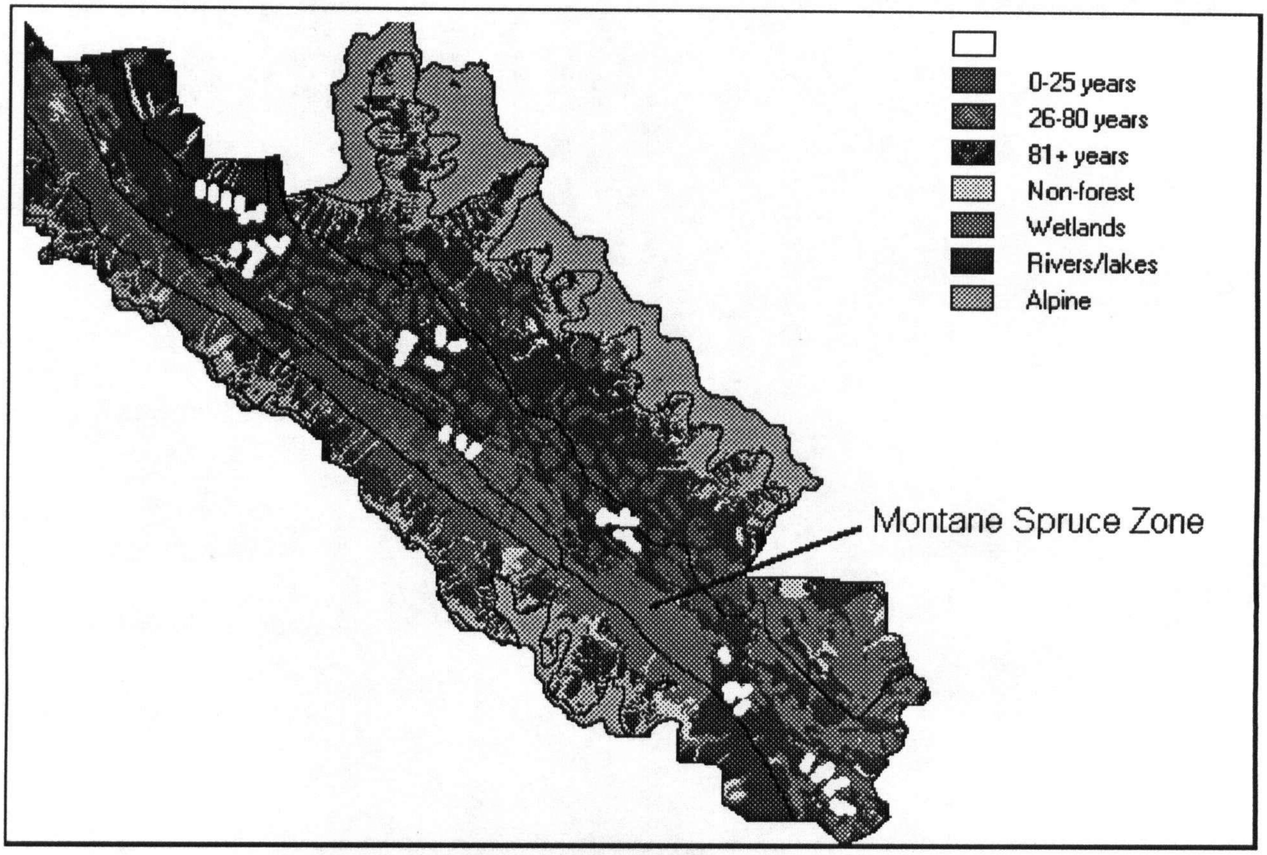

Figure 14: Location of bird point count locations (white circles) in the Beaverfoot study area.

Appendix 3. Scientific Names of Bird Species.

Table 13: Species codes, common names, and Latin names for bird species.

Species code	Common name	Latin name
AMRO	American robin	*Turdu migratorius*
BCCH	Black-capped chickadee	*Parus atricapillus*
BOCH	Boreal chickadee	*Parus hudsonicus*
BRCR	Brown creeper	*Certhia americana*
CHSP	Chipping sparrow	*Spizella passerina*
DEJU	Dark-eyed junco	*Junco hyemalis*
GCKI	Golden-crowned kinglet	*Regulus satrapa*
GRJA	Gray jay	*Perisoreus canadensis*
HAFL	Hammond's flycatcher	*Empidonax hammondii*
HAWO	Hairy woodpecker	*Picoides villosus*
MOCH	Mountain chickadee	*Parus atricapillus*
OCWA	Orange-crowned warbler	*Vermivora celata*
PISI	Pine siskin	*Carduelis pinus*
RBNU	Red-breasted nuthatch	*Sitta canadensis*
RCKI	Ruby-crowned kinglet	*Regulus calendula*
SOVI	Solitary vireo	*Vireo solitarius*
SPGR	Spruce grouse	*Dendragapus canadensis*
SWTH	Swainson's thrush	*Catharus ustulatus*
TOWA	Townsend's warbler	*Dendroica townsendi*
VATH	Varied thrush	*Ixoreus naevius*
VESP	Vesper's sparrow	*Pooecetes gramineus*
WAVI	Warbling vireo	*Vireo gilvus*
WIWA	Wilson's warbler	*Wilsonia pusilla*
WIWR	Winter wren	*Troglodytes troglodytes*
YRWA	Yellow-rumped warbler	*Dendroica coronata*

Appendix 4. Edge Contrast Matrix

Table 14: Edge contrast between forest and non-forest patches. 1 = high contrast forest edge; 0 = low contrast forest edge or non-forest edge. Adapted from Payne and Bryant (1994).

	CCUT	YOUN	OMAT	CMAT	DECI	UPLD	WTLD	WATR
CCUT	-							
YOUN	1	-						
OMAT	1	0	-					
CMAT	1	0	0	-				
DECI	1	0	0	0	-			
UPLD	0	0	1	1	1	-		
WTLD	0	1	1	1	1	0	-	
WATR	0	1	1	1	1	0	0	-

Appendix 5. Habitat Regression Models for 19.6 ha Circles.

Table 15: Bird community and population habitat regression models for the 19.6 ha concentric circles.

Bird Variables	Habitat Variables							Model	
	CCUT	YOUN	CORE	EDGE	NONF	EDGE	SIEI	R2	SEy
H			+	+		-	+	0.49	0.44
NSPP			+	+			+	0.45	1.53
TOTN		-	+					0.40	2.43
CHSP	+			-			+	0.45	0.53
DEJU	+							0.43	0.72
GCKI			+	+				0.43	0.40
TOWA			+	+				0.40	0.70
BRCR			+	+			-	0.30	0.20
VESP	+					-		0.30	0.26
SWTH	-	-		+	-			0.28	0.51
YRWA		+		+				0.27	0.46
RBNU	-	-		+				0.22	0.39
OCWA	+					-	+	0.22	0.35
VATH			+		+			0.18	0.30
BOCH			+					0.15	0.24
WIWA				+				0.14	0.17
RCKI				+				0.14	0.26
BCCH			+		+			0.13	0.28
AMRO						+		0.12	0.35
SOVI		+			+			0.10	0.19
MOCH				+				0.09	0.21
HAWO				+				0.06	0.17
WIWR			+					0.06	0.16
HAFL				+				0.06	0.16
GRJA				+				0.03	0.31

*Habitat models generated by stepwise regression analysis for the 250 m radius circles. n=117. PISI, SPGR, and WAVI did not have significant R^2. All regressions R^2 are significant at $p<.05$.