MONTANA STATE UNIVERSITY

Breeding bird communities in mature and old-growth Douglas-fir forests in southwest Montana
by James Robert Sparks

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
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Abstract:
This study was initiated to examine bird species diversity in mature and old-growth Douglas-fir ((Pseudotsuga menziesii) forests, due to the associated problems of timber harvest, forest fragmentation, and declining forest bird populations. Breeding bird communities were surveyed in four mature and four old-growth stands located on the Bozeman Ranger District, Gallatin National Forest during the months of June in 1988, 1989, and 1990. The study occurred within the Pine-Slushman Timber Sale Boundary in a heavily fragmented portion of the Bridger Mountain Range north of Bozeman, Montana. Birds were identified by territorial song, location calls, and visual observation during ten minute sampling periods. Margalef s, Berger-Parker, and Shannon diversity indices were used to make comparisons between stand types. A significance level of $P<0.05$ was used for statistical analysis. Bird species abundance, bird species diversity, bird genus diversity, and bird foraging guilds were significantly greater in old-growth stands than in mature stands. Bird species richness, bird family diversity, and bird nesting guilds were not significantly different between stand types although old-growth stands contained greater numbers of individuals and species in these categories than mature stands. Species such as the Cooper's hawk and red crossbill were found exclusively in mature stands and the redtailed hawk, American kestrel, Steller's jay, house wren, and white-crowned sparrow were found only in old-growth stands. The American robin, chipping sparrow, Lincoln's sparrow, Hammond's flycatcher, Williamson's sapsucker, northern flicker, hairy woodpecker, Cassin's finch, three-toed woodpecker, and Clark's nutcracker were found in both stand types, but with greater abundance in old-growth forests (scientific names for birds are located in Table 4). Mature and old-growth forests should be managed to facilitate the conservation and population viability of Neotropical migratory landbirds and resident birds. Vegetative management should emphasize harvest methods that promote the long-term retention of large live trees, multilayered overstories, large logs, and large snags. Forest management should strive towards "ecosystem management" objectives and consider equally the value of ecological, economical, and social attributes of the landscape. The limitations and strengths of the study are discussed, as well as the need for future research.

BREEDING BIRD COMMUNITIES IN MATURE AND OLD-GROWTH DOUGLAS-FIR FORESTS IN SOUTHWEST MONTANA

by

James Robert Sparks

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APPROVAL

of a thesis submitted by

James Robert Sparks

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date June 3, 1997

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ABSTRACT

This study was initiated to examine bird species diversity in mature and old-growth Douglas-fir ((*Pseudotsuga menziesii*) forests, due to the associated problems of timber harvest, forest fragmentation, and declining forest bird populations. Breeding bird communities were surveyed in four mature and four old-growth stands located on the Bozeman Ranger District, Gallatin National Forest during the months of June in 1988, 1989, and 1990. The study occurred within the Pine-Slushman Timber Sale Boundary in a heavily fragmented portion of the Bridger Mountain Range north of Bozeman, Montana. Birds were identified by territorial song, location calls, and visual observation during ten minute sampling periods. Margalef's, Berger-Parker, and Shannon diversity indices were used to make comparisons between stand types. A significance level of $P<0.05$ was used for statistical analysis. Bird species abundance, bird species diversity, bird genus diversity, and bird foraging guilds were significantly greater in old-growth stands than in mature stands. Bird species richness, bird family diversity, and bird nesting guilds were not significantly different between stand types although old-growth stands contained greater numbers of individuals and species in these categories than mature stands. Species such as the Cooper's hawk and red crossbill were found exclusively in mature stands and the red-tailed hawk, American kestrel, Steller's jay, house wren, and white-crowned sparrow were found only in old-growth stands. The American robin, chipping sparrow, Lincoln's sparrow, Hammond's flycatcher, Williamson's sapsucker, northern flicker, hairy woodpecker, Cassin's finch, three-toed woodpecker, and Clark's nutcracker were found in both stand types, but with greater abundance in old-growth forests (scientific names for birds are located in Table 4). Mature and old-growth forests should be managed to facilitate the conservation and population viability of Neotropical migratory landbirds and resident birds. Vegetative management should emphasize harvest methods that promote the long-term retention of large live trees, multilayered overstories, large logs, and large snags. Forest management should strive towards "ecosystem management" objectives and consider equally the value of ecological, economical, and social attributes of the landscape. The limitations and strengths of the study are discussed, as well as the need for future research.

INTRODUCTION

Douglas-fir forests in southwest Montana support breeding bird communities composed of Neotropical migratory landbirds and resident birds. Breeding Bird Surveys conducted by the United States Fish and Wildlife Service have indicated that certain Neotropical migratory and resident landbirds have experienced population declines during the past 26 years (Dobkin 1992, Robbins et al. 1992, Terborgh 1989, Ehrlich et al.1992). Many of these birds include forest songbirds that need large tracts of land on both United States breeding and winter grounds, and tropical winter habitat (Dobkin 1992). The conservation of populations of Neotropical migrant and resident songbirds depends on proactive land management (Sherry and Holmes 1992, Hunter et al. 1992, Niles 1992, Montana Partners in Flight 1997). In Montana, habitat changes that may result in the decline of bird species include livestock grazing, natural and prescribed fire, and commercial timber harvest (Bock et al. 1992, Dobkin 1992).

Livestock grazing has resulted in significant declines and increases in various songbirds inhabiting grasslands, riparian woodlands, and intermountain shrubsteppe ecosystems. However, little is known about the effects of grazing on bird communities in coniferous forests (Bock et al. 1992). Impacts associated with livestock grazing in forested environments are typically concentrated in riparian areas and grassy meadows (Sampson 1980). Livestock grazing in the western United States has contributed to

increases in the distribution and population of brown-headed cowbirds, a brood parasite of many Neotropiccal migratory birds (Mayfield 1965, Robbins et al. 1986, Robinson et al. 1992).

Natural and prescribed fire has the potential to affect bird communities (Rotenberry et al. 1992). Fires of various frequencies and intensities alter vegetation and may reduce available habitat for some birds, while creating insect outbreaks and providing foraging opportunities for other birds (Knight and Wallace 1989 as referenced in Bock et al. 1992). Ecological impacts associated with fire include changes in area climate and microclimate; composition, function, and structure of plant communities; and abundance and distribution of wildlife species (Bendell 1974). Species such as black-backed woodpeckers have been classified as fire-dependent birds, but long term studies on the relationships between birds and fire are generally lacking (Rotenberry et al. 1992).

Throughout the western United States commercial timber sales associated with sawlog production occur in mature and old-growth forests. Fragmentation of forest landscapes has been identified as a major problem for forest birds. Researchers in the eastern and western United States have identified declining breeding bird populations in North America (Whitcomb et al. 1981, Wilcove 1985, Finch 1991, Faaborg et al. 1992). Forest fragmentation increases edge habitat; brood parasitism from brown-headed cowbirds, and nest predation from avian and mammalian predators is significantly more common near forest edges (Dobkin 1992). Franklin et al. (1981) estimated that by 1980, less than five percent of the original forest land in the United States remained in old-

growth status. Harvesting mature forests reduces the potential for recruitment of old-growth stands in the landscape.

On the Gallatin National Forest, the Forest Plan directs managers to maintain various stages of vegetative succession in each compartment containing suitable timber for commercial harvest. A minimum of ten percent of each compartment will be maintained as grass/forb, shrub/seedling, pole/sapling, young, mature, and old-growth, respectively (Gallatin National Forest 1990). This management direction is based on the conservation of biological diversity, and in particular, the protection of old-growth forests.

Mature forests are defined as stands dominated by trees that have reached full development and seed production. On the Gallatin National Forest, Douglas-fir stands are estimated to reach maturity, or the culmination of growth, when trees are 120 years old (Gallatin National Forest 1987). Trees growing in mature stands express their maximum rate of diameter, height, and volume growth at this age. Old-growth forests are defined as multi-storied stands past full maturity (>120 years old) and showing signs of decadence; the last stage of forest succession. The structural attributes of old-growth Douglas-fir forests include stands with overstory trees at least 35 cm in diameter at breast height (dbh), ten to 40 percent crown closure in the overstory, a minimum of 35 tons per hectare of 7.5 cm diameter or larger course woody debris on the ground, at least two standing dead trees (snags) 35 cm dbh per hectare, and two or more canopy levels with a definite shrub/sapling layer (Franklin et al. 1981, Franklin and Spies 1984,Thomas et al. 1988, Warren 1990, Gallatin National Forest 1990).

The structural attributes of old-growth forests define their unique composition and functional characteristics; greater horizontal and vertical diversity within old-growth stands allow for wildlife niche specialization (Franklin and Spies 1991). However, wildlife species may not be unique to old-growth stands, although the diversity of species and associated interactions are considered different than in younger stands (Warren 1990). Many inventories of breeding birds indicate that there is a significant difference in bird species diversity between mature and old-growth forest communities while other studies reveal that there is no significant difference. Such conflicting results, which are summarized in the paragraphs below, add to the confusion and uncertainty of forest managers when prescribing activities in forest habitats.

Many studies on the habitat relationships of breeding birds suggest that a significant difference exists in breeding bird selection of mature and old-growth forests. In a literature review, Bull (1978) indicated that many studies revealed that up to 69 percent of breeding birds species inhabiting Douglas-fir forests nested in old-growth. She also found that some species, such as great gray owls and three-toed woodpeckers were more common in old-growth habitats. Studies in the Washington Cascade Range suggested that snag-dependent birds such as woodpeckers were not consistently more abundant in young, mature, or old-growth. However, cavity nesting birds such as Vaux's swift, chestnut-backed chickadees, red-breasted nuthatches, and brown creepers were more abundant in old-growth forests (Lundquist and Mariani 1991).

In a spring bird study in the Washington Cascade Range, results indicated that the highest detection rates of nesting avifauna occurred in old-growth while the lowest rates

occurred in mature Douglas-fir stands (Manuwal 1991). Studies on diurnal breeding birds in Oregon found that bark and hole nesting birds significantly selected Douglas-fir stands greater than 80 years old. These researchers also found that aerial and bark foraging birds reached their highest abundance in old-growth Douglas-fir (Huff and Raley 1991). In northwest California and southwest Oregon, Ralph et al. (1991) detected 14 species of breeding birds, including hairy woodpeckers, Hammond's flycatchers, gray jays, red-breasted nuthatches, and brown creepers, that reached peak abundance in older forests such as mature and old-growth Douglas-fir.

Studies in Montana have shown that old-growth stands have greater species abundance and richness of snag-dependent species than other age classes of forests (McClelland et al. 1979, Franklin et al. 1981, Marzluff and Lyon 1983). McClelland (1977) inventoried birds in western larch and Douglas-fir forests in northwestern Montana and found greater species richness in snag-dependent breeding birds such as Williamson's sapsuckers in old-growth forests. He also found that open-nesting species such as pine grosbeaks were more common in old-growth forests. In western Montana, researchers discovered more bird species in old-growth forests; individual species, including northern flickers, Swainson's thrushes, MacGillivray's warblers, western tanagers, and pine siskins were more abundant in old-growth stands. These researchers also found that Clark's nutcrackers, red-breasted nuthatches, chipping sparrows, brown-headed cowbirds, and red crossbills were more abundant in mature stands (Hejl and Woods 1989).

During the field season of 1991, Robin Moore, with assistance from Brad Elmore, completed the fourth year of this study. A compilation of the data, which includes four years of breeding bird data in harvest units, mature stands, and old-growth stands, indicated that total bird abundance was significantly greater in old-growth, but species richness did not differ between stands. Species such as the American robin and chipping sparrow were significantly more abundant in old-growth stands (Moore 1991).

Other research on the habitat relationships of breeding birds indicates that there is no significant difference in songbird selection of mature or old-growth habitats. Hutto et al. (1992), in a comparison review of four research studies, suggested that there was no consistent difference in bird species abundance between old-growth and mature second-growth stands. However, these researchers did find that six bird species, including hairy woodpeckers, brown creepers, and Swainson's thrushes were more abundant in old-growth stands. They also found that four species, including chipping sparrows and brown-headed cowbirds were more abundant in mature, second growth stands.

Studies in northwest California revealed that avian species richness did not differ in Douglas-fir forests of various ages including clear-cut units, young stands, mature sites, and old-growth forests (Raphael 1991). In Oregon, researchers found that during the nesting season, bird species diversity and total bird abundance was not significantly different in young, mature, and old-growth Douglas-fir stands (Carey et al. 1991, Gilbert and Allwine 1991). Mulqueen (1993) studied breeding birds south of Bozeman, Montana, and found that species diversity was significantly greater in selection-harvest stands than in clear-cut units or old-growth forests.

Innate behavior serves as the basis for habitat selection in birds (Wecker 1964, Hilden 1965, Lack 1968, Klopfer 1969). Proximate and ultimate causes of habitat selection relate to the functions of organisms (morphological, physiological, and biochemical aspects) and the evolutionary history that explains why an organism behaves the way it does, (Mayr 1961). For birds, habitat selection involves such proximate factors as landscape, terrain, nest sites, song posts, look-outs, feeding sites, drinking sites, other animals, and internal motivation that release a "settling reaction" in habitats (Hilden 1965). Ultimate or evolutionary responses for birds include food, structural and functional characteristics of the species, and shelter from predators and weather. Birds may also differentiate between suitable and optimal environments for habitat selection (Hilden 1965, Block 1993).

Bird species diversity shifts with changes in vegetative succession and is considered part of community succession (Pianka 1983). Bird species diversity consists of two interrelated components: species richness and species abundance. Species richness is defined as the number of species in a selected sampling unit. Species abundance is defined as the distribution of the number of individuals for each bird species (Magurran 1988). Bird species richness and abundance expand dramatically with increased horizontal and vertical structure of vegetation, as succession proceeds from early to late stages (Odum 1971).

There are latitudinal gradients of species diversity which indicate that species richness and abundance are greater near the equator and diminish in a predictable pattern, in both north and south directions, farther from the equator (Pianka 1983). Wildlife

communities with high species diversity may be more complex and therefore more stable than communities with low species diversity (Pimm 1991). Species diversity is also closely associated with habitat size. Larger areas have greater species richness and abundance than smaller areas (MacArthur and Wilson 1967). Spatial and temporal aspects of species diversity have also been identified. Spatial components include both horizontal and vertical resource partitioning of habitats by birds (MacArthur 1957, 1958, and 1960; MacArthur and MacArthur 1961; MacArthur et al. 1966). Temporal components include daily and seasonal resource partitioning (Pianka 1983).

Interactions between populations inhabiting communities may affect species diversity. Gause (1934) developed the principle of competitive exclusion stating that when two species are competing for the same limited resource, one species will be more efficient at utilizing those resources and eliminate the other species. This principle suggests that only dissimilar species would be expected to coexist in natural communities. However, ecologically similar species often occupy the same communities (MacArthur 1958, MacArthur et al. 1966).

The ecological niche, defined by Odum (1959) as an organism's "profession," determines its role in a community. An organism's fundamental niche, which is the range of conditions in which it potentially can live and replace itself, is rarely completely utilized under natural conditions. Instead, an organism's realized niche, which is the set of variables under which an organism actually exists in nature, generally restricts its numbers (Hutchinson 1957). Vegetation communities that are more diverse have greater bird species diversity because they contain a greater range of available resources. These

resources provide more niches, and component species are more abundant because they require smaller niches (Pianka 1983).

Behavior, morphology, and physiology may play an important role in bird species diversity in mature and old-growth Douglas-fir forests. Bird species richness and abundance may be different in regard to different stages of vegetative succession. When bird communities are examined for their hierarchical diversity, taxonomic distribution at the species, genus, and family level may differ in mature and old-growth forests. Pielou (1975) indicated that species diversity may be higher in communities composed of many genera instead of communities composed of only a few genera. Guilds may also play an important part in species diversity in mature and old-growth forests. Guilds comprise groups of species that inhabit a community and exploit similar resources in a related fashion, but do not necessarily belong to related taxonomic groups (Ehrlich et al. 1988). Food and nest sites are two important factors determining reproductive success for birds during the nesting season. Bird species comprising foraging and nesting guilds may exploit habitats similarly, but species diversity may be different in mature and old-growth stands.

During the spring, diurnal breeding birds are the most visible vertebrate group in forest communities. Therefore they were selected for inventory in this study. Due to associated problems of timber harvest, forest fragmentation, and declining bird populations, this study was initiated to examine bird species diversity in mature and old-growth Douglas-fir forests. These communities are commonly targeted for commercial

timber sales. Because of the interrelationships between proximate and ultimate causes, ecological niche, and species diversity, the hierarchical diversity and the foraging and nesting guilds of birds were examined.

It was the intention of this study to determine the value of mature and old-growth Douglas-fir stands to breeding bird communities and to comment on forest practices that may be detrimental to bird communities. Recommendation on mitigation techniques to lessen impacts associated with timber harvest and suggestions regarding proactive management of Neotropical migratory landbirds and resident birds will also be discussed. Such information is intended to help forest managers make appropriate decisions to benefit the conservation of forest birds.

STUDY AREA

The study area was located along the east side of the Bridger Mountain Range on the Bozeman Ranger District, Gallatin National Forest, 24 kilometers north of Bozeman, Montana (Figure 1). Legal description for the project area is T1N, R6E, Section 1; T1N, R7E, Section 6; T2N, R6E, Section 36; and T2N, R7E, Section 36. All Douglas-fir stands selected for study were located within the Pine-Slushman Timber Sale Boundary south of Bridger Bowl Ski Area. All logging in the timber sale was accomplished in 1985 and 1986, two years prior to the initiation of the study. The vicinity around and within the study site has been heavily fragmented as a result of numerous timber sales. Harvesting methods were predominantly clear-cut and selective-cut units that are located on public and private land.

The Bridger Mountains are oriented in a north-south direction. The west side of the range is steep and dry with sparsely vegetated south aspects and densely forested north aspects on spur ridges. The east side of the Bridger Range, the area where the study occurred, is less steep, receives more precipitation, and consequently supports more productive forests with dense stands of conifers. Consequently, timber harvest activity has been heavier on the east side than on the west side of the range.

The landscape in this portion of the Bridger Range is characterized by gently rolling to moderately steep, structurally controlled slopes and colluvial deposits. Bedrock consists of thick beds of dark colored sandstone that are interbedded with thin layers of shale and siltstone. All bedrock material is part of the Livingston group deposited during

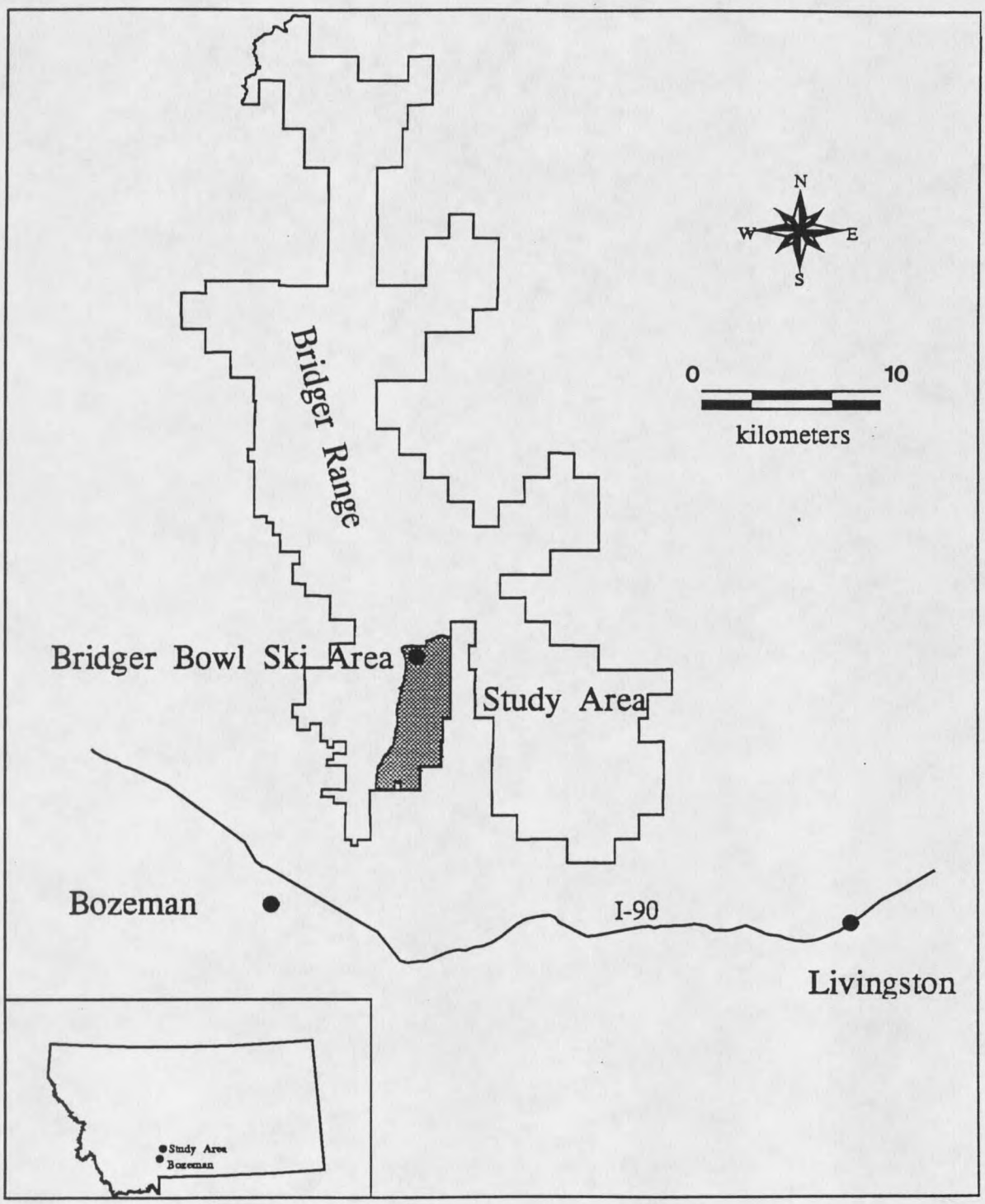


Figure 1. Map of the study area located in the Bridger Range, north of Bozeman. Montana.

the Tertiary age. Bedrock composed of volcanic material is also present and is composed of hard crystalline rocks which occur as dikes and sills on ridgetops (Davis and Shovic 1984).

Soils consist of light colored and darkened surface layers of fine to medium textured material formed from weathered sandstone, shale, and volcanic material. All soils in the area are well drained. Conditions associated with coniferous forest habitats developed soils that are dark grayish brown with gravelly loam surface layers 23 cm thick. Subsoils tend to be yellowish brown in color with cobbly clay loam extending approximately 73 cm thick. Substratum soils are pale brown, stony loams that overlie the bedrock at depths of 1.2 m to over 1.5 m. Mollic Cryoboralfs, loamy skeletal mixes, and Typic Cryoboralfs are the dominant soil types that developed under coniferous forest vegetation (Davis and Shovic 1984).

Elevations range from 1,800 m to over 3,000 m in the Bridger Mountains, but generally are from 1,800 m to 2,200 m in the study area. Slopes in the mountain range are gentle to rolling to very steep; they typically vary from 0 to 90 %. In the project area, stands selected for study range from 20 % to 40%. Aspects are variable throughout the east side of the Bridger Range, but higher elevations have predominantly eastern aspects while lower elevations vary from north, east, south, and west (Table 1).

Forest overstory vegetation consists of dense stands composed of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmanni*), and subalpine fir (*Abies lasiocarpa*). Stands selected for study were composed primarily of Douglas-fir with varying amounts of

Table 1. Stand descriptions based on timber stand data base information available at the Bozeman Ranger District.

Stand	Stand Type	Area (Hectares)	Elevation (Meters)	Aspect	Slope	Habitat * Type
1	Mature	26	1,982	N	20 %	281, 323
2	Mature	15	1,951	NE-SE	30 %	281, 313
3	Mature	32	1,951	SE	30 %	281, 313
4	Mature	32	1,951	E	30 %	262, 312
5	Old-Growth	18	1,951	W	40 %	312
6	Old-Growth	14	1,890	SE	20 %	330
7	Old-Growth	60	2,195	E	30 %	792
8	Old-Growth	36	2,195	E	25 %	792

* Habitat Type Definitions (Pfister et al. 1977):

262 - *Pseudotsuga menziesii / Physocarpus malvaceus - Calamagrostis rubescens*
281 - *Pseudotsuga menziesii / Vaccinium globulare - Vaccinium globulare*
312 - *Pseudotsuga menziesii / Symphoricarpos albus - Calamagrostis rubescens*
313 - *Pseudotsuga menziesii / Symphoricarpos albus - Symphoricarpos albus*
323 - *Pseudotsuga menziesii / Calamagrostis rubescens - Calamagrostis rubescens*
330 - *Pseudotsuga menziesii / Carex geyeri*
792 - *Abies lasiocarpa / carex geyeri - Pseudotsuga menziesii*

lodgepole pine and subalpine fir. Understory shrubs consist of ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos albus*), white spiraea (*Spiraea betulifolia*), globe huckleberry (*Vaccinium globulare*), and Rocky Mountain maple (*Acer glabrum*). Understory herbaceous plants and grasses include heartleaf arnica (*Arnica cordifolia*), mountain bluebell (*Mertensia ciliata*), Indian paintbrush (*Castilleja sp.*), pine grass (*Calamagrostis rubescens*), and elk sedge (*Carex geyeri*). (Bozeman Ranger District files).

Guidelines described by the Gallatin National Forest for mature and old-growth stands were used to categorize mature and old-growth stands. Tree age, diameter at breast height (dbh) for live trees, number of large cavity trees per hectare, tons per hectare of 7.5 cm. dbh or larger coarse woody debris, percent crown closure, and number of canopy layers were the primary stand variables used to differentiate between mature and old-growth stands (Table 2).

Overstory trees in old-growth stands were 100 to 200 years older than the oldest trees in mature stands. The maximum age of trees in old-growth stands was 350 years, while the maximum age of trees in mature stands was 145 years. The range of tree ages was greater in old-growth stands. The size and range of live tree diameters at breast height (dbh) were greater in old-growth stands. The largest live tree diameters were 88 cm for mature and 113 cm for old-growth stands. The number of large cavity trees and tons per hectare of woody debris greater than 7.5 cm was greater in old-growth than in mature stands. Crown closure was less in old-growth stands which created more canopy gaps than in mature stands. Canopy layers were also more abundant in old-growth stands and ranged from 2-3 layers. Canopy layers in mature stands ranged from 1-2 layers.

The climate of the Bridger Range is typical of southwestern Montana mountains. Information on temperature, precipitation, and snow depth was collected from the Bridger Bowl and Bangtail Ridge SNOTEL sites located in the study area and 12 kilometers north, respectively. The average temperature during June (breeding bird study month) is 9 C, with an average maximum temperature of 19 C and an average minimum temperature of 1 C. The average precipitation for June is 13 cm and ranges from a maximum of 26 cm to a

minimum of 0.5 cm. The average mid-month measurement for snow depth during June is 15 cm, with a maximum snow depth of 97 cm and a minimum of 0 cm. During the study period from 1988-1990, the average June temperature, precipitation, and snow depth were 10 C, 9 cm, and 0 cm, respectively (Natural Resource Conservation Service files). However, patches of snow remained in shaded areas until mid-June each year of the study.

Recent historic impacts that have occurred in the study area include wildfire, timber harvest, and livestock grazing. In Douglas-fir cover types (fire group 6), recurrent fires kept stands open and mean fire intervals were 42 years. In Douglas-fir/lodgepole pine mixed cover types (fire group 7), fires burned hot and stand replacement events occurred every 150-200 years. The most recent large stand replacement fires occurred in the area approximately 100 years ago (Bozeman Ranger District 1996). Charred logs and fire scars on living trees can be found in the area.

Timber harvest began at the turn of the century, but increased dramatically on private and public land during the 1970's and 1980's. Forested areas in the vicinity are extremely fragmented as a result of timber harvest activity and associated road building, and development of the Bridger Bowl Ski Area. Timber sales are currently being accomplished and are planned to continue in the near future.

Livestock grazing has a long history in the Bridger Mountains and began in the late 1800's. Both sheep and cattle grazed in the area during the past. Currently, the majority of the study area is grazed by 65 yearling cattle which are part of the Pine Creek Grazing Allotment. Livestock grazing occurs from July 1 to September 30 (Bozeman Ranger District 1996). No cattle were present on the allotment during the breeding bird survey.

Table 2. Vegetative characteristics based on timber stand data base information available at the Bozeman Ranger District.

Stand	Tree * Species %	Trees / Hectare	Age Range Years	Height Range Meters	DBH ** Range Cm.	Cavity Trees / Hectare	Wood *** Debris / Hectare	Canopy Layers	Crown Ratio %	Crown Cover %
1	DF: 84 LP: 16	DF: 57 LP: 17	DF: 110-130 LP: 90-100	DF: 23-27 LP: 23-27	All Sp. 23-43	0.12, $\bar{x}$ dbh = 34 cm	4 Tons	1	DF: 30 LP: 30	60
2	DF: 65 LP: 35	DF: 43 LP: 22	DF: 65-145 LP: 48-120	DF: 12-32 LP: 17-29	All Sp. 18-73	0.73, $\bar{x}$ dbh = 29 cm	1 Tons	2	DF: 30 LP: 30	70
3	DF: 93 LP: 7	DF: 54 LP: 5	DF: 75-125 LP: 70- 89	DF: 14-33 LP: 20-38	All Sp. 23-68	0.22, $\bar{x}$ dbh = 34 cm	5 Tons	2	DF: 35 LP: 32	60
4	DF: 91 LP: 9	DF:142 LP: 4	DF: 80-130 LP: 80-130	DF: 17-27 LP: 17-27	All Sp. 13-88	0.31, $\bar{x}$ dbh = 37 cm	5 Tons	1	DF: 30 LP: 30	70
5	DF: 98 LP: 2	DF:146 LP: 3	DF: 85-250 LP: 85-135	DF: 17-27 LP: 17-27	All Sp. 15-113	1.50, $\bar{x}$ dbh = 57 cm	3 Tons	2	DF: 50 LP: 50	40
6	DF: 100	DF: 14	DF: 90-250	DF: 16-26	DF: 20-78	3.30, $\bar{x}$ dbh = 48 cm	5 Tons	2	DF: 50	20

Table 2. (Continued)

Stand	Tree * Species %	Trees / Hectare	Age Range Years	Height Range Meters	DBH ** Range Cm.	Cavity Trees / Hectare	Wood *** Debris / Hectare	Canopy Layers	Crown Ratio %	Crown Cover %
7	DF: 80 AF: 20	DF: 27 AF: 9	DF: 70-350 AF: 35- 80	DF: 13-27 AF: 10-18	All Sp. 20-105	0.72, $\bar{x}$ dbh = 50 cm	7 Tons	3	DF: 40 AF: 50	55
8	DF: 62 AF: 38	DF: 21 AF: 13	DF: 80-350 AF: 40- 85	DF: 27-30 AF: 12-20	All Sp. 13-100	1.06, $\bar{x}$ dbh = 41 cm	8 Tons	3	DF: 40 AF: 50	45

* Tree Species: AF = Subalpine fir (*Abies lasiocarpa*), DF = Douglas-fir (*Pseudotsuga menziesii*), LP = Lodgepole pine (*Pinus contorta*).

** Diameter at Breast Height: all species included.

*** Woody debris consists of downed material 7.5 cm or greater in diameter.

METHODS

Site Selection

The project area was selected within the boundaries of the Pine-Slushman Timber Sale. The study was financed with Knutson-Vandenberg (K-V) funds which were obtained through timber receipt dollars in conjunction with this sale. The guidelines for using K-V funds state that all activities such as regeneration, improvements, and monitoring must be accomplished within the Sale Area Boundary. Therefore, selection of the number, type, and size of Douglas-fir stands for the study was limited to those stands available within the Sale Area Boundary.

A copy of the Sale Area map, topographic maps, aerial photographs, and stand exam data were used to select study sites. Once stands were identified, they were examined in the field for mature and old-growth characteristics. Those areas that were dominated by Douglas-fir trees in the overstory and close to or greater than 20 hectares in size were chosen for the project. Eight Douglas-fir stands were selected for the study, representing four mature and four old-growth sites. The eight sites were all natural fire-regenerated stands that developed under unmanaged conditions. Prior to extensive timber harvest, understory and/or stand replacement wildfire was the force of disturbance that shaped the area.

Birds

Data collection

To inventory bird species diversity, the abundance and variety of species in mature and old-growth Douglas-fir stands, three permanent 100 m radius circles (points) were placed in each of the four mature and four old-growth stands. Each stand was visited before the survey was initiated and points were established and marked with survey stakes. Points were selected by walking through each stand and measuring the distance from the stand's edge and between points. A minimum distance of 100 m was measured from point center to any portion of the stand's edge and all points were placed 200 m apart.

Each stand was surveyed six times each year, from May 31 to July 1, during 1988, 1989, and 1990. Birds were inventoried only during morning hours. Three sampling periods were established for the survey: early morning from 0600 to 0800, mid-morning from 0800 to 0930, and late morning from 0930 to 1100 hours. Each stand was visited twice during each of the three sampling periods in 1988, 1989, and 1990. During these sampling periods, the direction of the survey was reversed and conducted from point 1 to point 3 on one visit and from point 3 to point 1 on the next visit for each of the early, mid, and late morning surveys. A minimum of three days was required to pass before a stand was revisited.

The survey was conducted using point count methods developed by Hutto et al. (1986). Birds were recorded at each point for ten minutes. Only those birds heard (location calls and/or songs) or seen in the stand and within a 100 m radius of the

point center were recorded. Birds flying over a point or heard beyond the 100 m radius of a point were not recorded. For example, species such as pine siskins and red crossbills, which frequently flew over stands without landing, were not recorded. An effort was made not to duplicate individual birds at a point and only first detections were recorded. Birds flushed from within a stand while walking between points were recorded. Inventories were conducted only on days with little or no precipitation and only when wind speeds were less than 25 kilometers per hour.

Data Analysis

Bird species abundance, bird species richness, hierarchical diversity, bird foraging guilds, and bird nesting guilds were analyzed to determine if there was a difference between mature and old-growth Douglas-fir stands. Bird species abundance was analyzed by calculating the mean abundance of the total number of individual birds that were recorded during the three year study period. A two-sampled t-test was used to determine if bird species abundance was significantly different between mature and old-growth stands. Bird species richness was calculated as the mean number of total bird species recorded per stand during the three year study period. A two-sampled t-test was used to determine if bird species richness was significantly different between mature and old-growth stands.

Three diversity indices were used to make comparisons and to determine if there were differences between mature and old-growth stands based on hierarchical diversity, bird foraging guilds, and bird nesting guilds. Margalef's diversity index was the simplest

test used and was calculated by combining the total number of bird species and individuals recorded during the three year study period. Margalef's index is weighted towards species richness (Magurran 1988). The Berger-Parker diversity index was also used and is based on the proportional abundance of bird species. This index is considered a non-parametric index and is referred to as a dominance measure because results are weighted towards the abundance of the most common species rather than species richness (Magurran 1988).

The third index used was the Shannon diversity index which is also based on the proportional abundance of bird species. This index is one of the most commonly used to measure diversity. The Shannon index is considered an information theory index based on the principle that diversity in a natural system can be measured similarly to the information contained in a message (Magurran 1988). A two-tailed t-test was used to determine if there was a significant difference between the Shannon diversity index for mature and old-growth stands. The methods used for determining the Shannon diversity index and the two-tailed t-test are found in Magurran (1988).

Hierarchical diversity was examined at three taxonomic levels. Differences in bird species diversity, bird genus diversity, and bird family diversity were investigated in each stand type using Margalef's, Berger-Parker, and Shannon diversity indices. Statistical tests were not used to compare results for Margalef's or the Berger-Parker diversity index. A t-test was used to compare for significant differences in the Shannon diversity indexes for both stand types. These diversity indices were also applied to bird foraging and nesting guild comparisons. Information used for categorizing birds by foraging and nesting guilds was obtained from Ehrlich et al. (1988) and DeGraaf et al. (1991) (Table 3).

Table 3. Foraging and nesting guilds for birds utilized in the analysis.*

Bird Species	Foraging Guilds **				Nesting Guilds ***			
	GR	FO	BA	AE	GN	SH	TR	SN
Sharp-shinned Hawk				X			X	
Cooper's Hawk				X			X	
Red-tailed Hawk				X			X	
American Kestrel				X				X
Blue Grouse	X				X			
Great Gray Owl				X			X	
Williamson's Sapsucker			X					X
Hairy Woodpecker			X					X
Three-toed Woodpecker			X					X
Northern Flicker	X							X
Hammond's Flycatcher				X			X	
Gray Jay	X						X	
Steller's Jay	X						X	
Clark's Nutcracker		X					X	
Mountain Chickadee		X						X
Red-breasted Nuthatch			X					X
Brown Creeper			X					X
House Wren	X							X
Ruby-crowned Kinglet		X					X	
Townsend's Solitaire				X	X			

Table 3. (Continued)

Bird Species	Foraging Guilds **				Nesting Guilds***			
	GR	FO	BA	AE	GN	SH	TR	SN
Swainson's Thrush		X				X		
Hermit Thrush	X				X			
American Robin	X						X	
Warbling Vireo		X					X	
Yellow-rumped Warbler		X					X	
MacGillivray's Warbler		X				X		
Western Tanager		X					X	
Chipping Sparrow	X						X	
Lincoln's Sparrow	X				X			
White-crowned Sparrow	X					X		
Dark-eyed Junco	X				X			
Brown-headed Cowbird****	X							
Pine Grosbeak		X					X	
Cassin's Finch	X						X	
Red Crossbill		X					X	
Pine Siskin		X					X	
Evening Grosbeak	X						X	

* Foraging and nesting guild classifications based on information from Ehrlich et al. (1988) and DeGraaf et al. (1991).

** Foraging Guild
GR = Ground Gleaner
FO = Foliage Gleaner
BA = Bark Gleaner
AE = Aerial Forager

*** Nesting Guild
GN = Ground Nester
SH = Shrub Nester
TR = Tree Nester
SN = Snag Nester

**** Brown-headed Cowbird is a brood parasite.

A t-test was used to determine if there were significant differences in the Shannon diversity index for mature and old-growth stands, but statistical tests were not used for Margalef's or the Berger-Parker index results. Bird species were categorized into four foraging guilds including aerial foragers, ground gleaners, bark gleaners, and foliage gleaners. Birds were also categorized into five nesting guilds which included brood parasites, ground nesters, shrub nesters, snag nesters, and tree nesters.

RESULTS

During the three year study, 52 bird species were detected in the study area (Table 4). Of these birds, eight species were heard or seen within the Pine-Slushman Timber Sale Boundary, but were not recorded in any of the monitored stands. Forty-five bird species were detected in mature and old-growth stands. Of these birds, seven species were recorded only once during the survey period and were considered accidental or extremely rare. The above mentioned 15 species were excluded from analysis and only species recorded more than once were analyzed. Therefore, a total of 37 bird species were considered for analysis representing 25 Neotropical migratory and 12 resident landbirds.

Bird Species Abundance

A total of 3,493 individual birds was recorded during 1988, 1989, and 1990 (Table 5). The total number of individual birds recorded during the three year study was greater in each of the four old-growth Douglas-fir stands than in each of the four mature Douglas-fir stands. Total bird species abundance in mature stands represented 1,498 individuals; total bird species abundance in old-growth stands represented 1,995 individuals. Mean bird species abundance was 375 (range: 327-422) and 499 (range: 454-568) individuals in mature and old-growth stands, respectively (Table 6). A two-sampled t-statistic determined that mean bird species abundance by stand type was significantly greater in old-growth stands than in mature stands ($t = 3.87$, $df = 6$, $P = 0.008$). Calculations for

bird species abundance were based on the mean total number of individual birds recorded per stand during the three year study for mature and old-growth stands.

Table 4. Cumulative list of all bird species seen in the study area (1988-1990). *

Common Name	Scientific Name	Family	Status
Sharp-shinned Hawk **	*Accipiter striatus*	Accipitridae	Neotropical
Cooper's Hawk	*Accipiter cooperii*	Accipitridae	Neotropical
Northern Goshawk	*Accipiter gentilis*	Accipitridae	Neotropical
Red-tailed Hawk	*Buteo jamaicensis*	Accipitridae	Neotropical
Golden Eagle	*Aquila chrysaetos*	Accipitridae	Neotropical
American Kestrel	*Falco sparverius*	Falconidae	Neotropical
Blue Grouse	*Dendragapus obscurus*	Phasianidae	Resident
Ruffed Grouse	*Bonasa umbellus*	Phasianidae	Resident
Great Horned Owl	*Bubo virginianus*	Strigidae	Resident
Great Gray Owl	*Strix nebulosa*	Strigidae	Resident
Red-naped Sapsucker	*Sphyrapicus nuchalis*	Picidae	Neotropical
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Picidae	Neotropical
Hairy Woodpecker	*Picoides villosus*	Picidae	Resident
Three-toed Woodpecker	*Picoides tridactylus*	Picidae	Resident
Northern Flicker	*Colaptes auratus*	Picidae	Neotropical
Pileated Woodpecker	*Dryocopus pileatus*	Picidae	Resident
Olive-sided Flycatcher	*Contopus borealis*	Tyrannidae	Neotropical
Western Wood-pewee	*Contopus sordidulus*	Tyrannidae	Neotropical
Hammond's Flycatcher	*Empidonax hammondii*	Tyrannidae	Neotropical
Tree Swallow	*Tachycineta bicolor*	Hirundinidae	Neotropical
Gray Jay	*Perisoreus canadensis*	Corvidae	Resident
Steller's Jay	*Cyanocitta stelleri*	Corvidae	Resident
Clark's Nutcracker	*Nucifraga columbiana*	Corvidae	Resident
Common Raven	*Corvus corax*	Corvidae	Resident
Mountain Chickadee	*Parus gambeli*	Paridae	Resident
Red-breasted Nuthatch	*Sitta canadensis*	Sittidae	Resident
Brown Creeper	*Certhia americana*	Certhiidae	Neotropical
House Wren	*Troglodytes aedon*	Troglodytidae	Neotropical
Golden-crowned Kinglet	*Regulus satrapa*	Muscicapidae	Neotropical
Ruby-crowned Kinglet	*Regulus calendula*	Muscicapidae	Neotropical
Mountain Bluebird	*Sialia currucoides*	Muscicapidae	Neotropical
Townsend's Solitaire	*Myadestes townsendi*	Muscicapidae	Neotropical
Swainson's Thrush	*Catharus ustulatus*	Muscicapidae	Neotropical
Hermit Thrush	*Catharus guttatus*	Muscicapidae	Neotropical

Table 4. (Continued)

Common Name	Scientific Name	Family	Status
American Robin	*Turdus migratorius*	Muscicapidae	Neotropical
Warbling Vireo	*Vireo gilvus*	Vireonidae	Neotropical
Orange-crowned Warbler	*Vermivora celata*	Emberizidae	Neotropical
Yellow-rumpedWarbler	*Dendroica coronata*	Emberizidae	Neotropical
MacGillivray's Warbler	*Oporornis tolmiei*	Emberizidae	Neotropical
Western Tanager	*Piranga ludoviciana*	Emberizidae	Neotropical
Black-headed Grosbeak	*Pheucticus melanocephalus*	Emberizidae	Neotropical
Lazuli Bunting	*Guiraca caerulea*	Emberizidae	Neotropical
Chipping Sparrow	*Spizella passerina*	Emberizidae	Neotropical
Lincoln's Sparrow	*Melospiza lincolnii*	Emberizidae	Neotropical
White-crownedSparrow	*Zonotrichia leucophrys*	Emberizidae	Neotropical
Dark-eyed Junco	*Junco hyemalis*	Emberizidae	Neotropical
Brown-headed Cowbird	*Molothrus ater*	Emberizidae	Neotropical
Pine Grosbeak	*Pinicola enucleator*	Fringillidae	Resident
Cassin's Finch	*Carpodacus cassinii*	Fringillidae	Neotropical
Red Crossbill	*Loxia curvirostra*	Fringillidae	Resident
Pine Siskin	*Carduelis pinus*	Fringillidae	Neotropical
Evening Grosbeak	*Coccothraustes vespertinus*	Fringillidae	Resident

* Species, sequence, and spelling follow the American Ornithologists' Union Check-list of North American Birds, Sixth Edition (1995).

** Birds in bold print were used during the analysis (37 species).

Birds recorded in mature and old-growth forest stands were ranked by abundance from most common to least common species (Table 7). Bird species abundance exhibited a truncated distribution of records from very common to rare. Species such as dark-eyed

Table 5. Total number of individuals of each of the 37 bird species studied in four mature and four old-growth Douglas-fir stands (1988-1990).

Bird Species	Mature Douglas-fir				Old-Growth Douglas-fir			
	1988	1989	1990	Total	1988	1989	1990	Total
Sharp-shinned Hawk	1	0	1	2	2	0	1	3
Cooper's Hawk	0	0	4	4	0	0	0	0
Red-tailed Hawk	0	0	0	0	1	0	1	2
American Kestrel	0	0	0	0	3	0	0	3
Blue Grouse	1	0	0	1	0	3	0	3
Great Gray Owl	2	1	1	4	1	0	1	2
Williamson's Sapsucker	1	0	0	1	6	7	5	18
Hairy Woodpecker	3	0	3	6	5	6	4	15
Three-toed Woodpecker	0	0	1	1	5	5	2	12
Northern Flicker	0	3	1	4	4	12	1	17
Hammond's Flycatcher	1	0	0	1	7	11	8	26
Gray Jay	15	9	6	30	12	10	11	33
Steller's Jay	0	0	0	0	2	8	5	15
Clark's Nutcracker	3	1	0	4	4	7	0	15
Mountain Chickadee	32	33	27	92	40	48	40	128
Red-breasted Nuthatch	48	61	32	141	47	55	35	137
Brown Creeper	16	16	13	45	16	11	19	46
House Wren	0	0	0	0	17	4	4	25
Ruby-crowned Kinglet	30	31	43	104	34	71	42	147
Townsend's Solitaire	1	1	6	8	2	1	10	13

Table 5. (Continued)

Bird Species	Mature Douglas-fir				Old-Growth Douglas-fir			
	1988	1989	1990	Total	1988	1989	1990	Total
Swainson's Thrush	39	7	16	62	25	18	9	52
Hermit Thrush	5	3	5	13	1	5	2	8
American Robin	28	25	9	62	57	48	33	138
Warbling Vireo	38	30	36	104	33	23	26	82
Yellow-rumped Warbler	76	92	78	246	45	87	63	195
MacGillivray's Warbler	14	17	10	41	29	24	18	71
Western Tanager	63	51	46	160	68	76	55	199
Chipping Sparrow	6	9	8	23	34	37	23	94
Lincoln's Sparrow	4	1	6	11	8	13	11	32
White-crowned Sparrow	0	0	0	0	9	11	2	22
Dark-eyed Junco	70	72	74	216	78	89	112	280
Brown-headed Cowbird	25	10	7	42	28	19	17	64
Pine Grosbeak	1	0	0	1	1	0	0	1
Cassin's Finch	2	2	1	5	9	0	6	15
Red Crossbill	0	0	2	2	0	0	0	0
Pine Siskin	35	5	20	60	33	10	33	76
Evening Grosbeak	2	0	0	2	1	4	1	6
Totals	562	480	456	1,498	667	723	600	1,995

juncos, yellow-rumped warblers, and western tanagers were considered very common (>300 observations); species such as chipping sparrows, warbling vireos, and pine siskins were considered common (>100 observations); and species such as three-toed woodpeckers, sharp-shinned hawks, and great gray owls were considered uncommon or rare (<20 observations).

Table 6. Abundance of individual birds and mean number of birds recorded per stand in mature and old-growth Douglas-fir stands (1988-1990).

Stand Number	Total Number of Individuals Per Stand (Per Year)			Total Number of Individuals Per Stand (Combined Years)	
Mature Douglas-fir	1988	1989	1990	1988-1990	Mean *
1	130	109	88	327	375
2	135	111	115	361	
3	146	144	132	422	
4	149	118	121	388	
Old-Growth Douglas-fir					
5	194	159	119	472	499
6	170	156	128	454	
7	145	188	168	501	
8	162	220	186	568	

* Mean number of individual birds recorded in mature and old-growth Douglas-fir stands.

Table 7. Rank and abundance tabulated for 37 bird species studied in four mature (N = 1,498) and four old-growth (N = 1,995) Douglas-fir stands (1988-1990).

Mature Douglas-fir		Old-Growth Douglas-fir	
Bird Species Rank	Total	Bird Species Rank	Total
1. Yellow-rumped Warbler	246	1. Dark-eyed Junco	280
2. Dark-eyed Junco	216	2. Western Tanager	199
3. Western Tanager	160	3. Yellow-rumped Warbler	195
4. Red-breasted Nuthatch	141	4. Ruby-crowned Kinglet	147
5. Ruby-crowned Kinglet	104	5. American Robin	138
6. Warbling Vireo	104	6. Red-breasted Nuthatch	137
7. Mountain Chickadee	92	7. Mountain Chickadee	128
8. Swainson's Thrush	62	8. Chipping Sparrow	94
9. American Robin	62	9. Warbling Vireo	82
10. Pine Siskin	60	10. Pine Siskin	76
11. Brown Creeper	45	11. MacGillivray's Warbler	71
12. Brown-headed Cowbird	42	12. Brown-headed Cowbird	64
13. MacGillivray's Warbler	41	13. Swainson's Thrush	52
14. Gray Jay	30	14. Brown Creeper	46
15. Chipping Sparrow	23	15. Gray Jay	33
16. Hermit Thrush	13	16. Lincoln's Sparrow	32
17. Lincoln's Sparrow	11	17. Hammond's Flycatcher	26
18. Townsend's Solitaire	8	18. House Wren	25
19. Hairy Woodpecker	6	19. White-crowned Sparrow	22
20. Cassin's Finch	5	20. Williamson's Sapsucker	18
21. Cooper's Hawk	4	21. Northern Flicker	17
22. Great Gray Owl	4	22. Hairy Woodpecker	15
23. Northern Flicker	4	23. Cassin's Finch	15
24. Clark's Nutcracker	4	24. Steller's Jay	15
25. Sharp-shinned Hawk	2	25. Townsend's Solitaire	13
26. Red Crossbill	2	26. Clark's Nutcracker	15
27. Evening Grosbeak	2	27. Three-toed Woodpecker	12
28. Blue Grouse	1	28. Hermit Thrush	8
29. Williamson's Sapsucker	1	29. Evening Grosbeak	6
30. Three-toed Woodpecker	1	30. Sharp-shinned Hawk	3
31. Hammond's Flycatcher	1	31. Blue Grouse	3
32. Pine Grosbeak	1	32. American Kestrel	3
33. Red-tailed Hawk	0	33. Great Gray Owl	2
34. American Kestrel	0	34. Red-tailed Hawk	2
35. Steller's Jay	0	35. Pine Grosbeak	1
36. House Wren	0	36. Cooper's Hawk	0
37. White-crowned Sparrow	0	37. Red Crossbill	0

Bird Species Richness

Of the 37 bird species recorded, 35 species were detected in old-growth forests and 32 species were recorded in mature stands. Mean bird species richness was 23 (range: 19-26) and 28 (range: 22-31) species in mature and old-growth stands, respectively (Table 8). A two-sampled t-statistic determined that mean bird species richness by stand type was not significantly different between mature and old-growth stands ($t = 1.00$, $df = 6$, $P = 0.317$). Calculations for bird species richness were based on the mean total number of bird species recorded per stand during the three year study for mature and old-growth stands.

Table 8. Number of bird species and mean number of bird species recorded per stand in mature and old-growth Douglas-fir stands (1988-1990).

Stand Number	Total Number of Species Per Stand (By Year)			Total Number of Species Per Stand (Combined Years)	
Mature Douglas-fir	1988	1989	1990	1988-1990	Mean *
1	21	16	19	26	23
2	18	16	18	23	
3	17	17	17	19	
4	21	15	19	24	
Old-Growth Douglas-fir					
5	19	18	18	22	28
6	26	20	23	28	
7	22	25	25	30	
8	28	24	22	31	

* Mean total number of bird species recorded per stand during three years of study for mature and old-growth Douglas-fir stands.

Although their numbers were low, Cooper's hawks (N = 4) and red crossbills (N = 2) were found only in mature stands. Species found only in old-growth stands included red-tailed hawks (N = 2) , American kestrels (N = 3), Steller's jays (N = 15), house wrens (N = 25), and white-crowned sparrows (N = 22). Although frequencies varied, all of the remaining 30 species were found in both mature and old-growth stands.

Hierarchical Diversity

Bird species diversity, measured by combining total bird species abundance and richness, was found to be greater in old-growth than in mature Douglas-fir stands (Table 9). Calculations for diversity indices were based on the total number of bird species and the total number of individuals per species recorded during the three year study in mature and old-growth stands. Margalef's diversity index was estimated as Dmg = 4.24 and Dmg = 4.47 for mature and old-growth stands, respectively. The Berger-Parker diversity index calculated for mature stands was d = 0.16 and for old-growth stands was d = 0.14. The reciprocal of the Berger-Parker index was 1/d = 6.25 for mature and 1/d = 7.14 for old-growth stands.

The Shannon diversity index was estimated as H' = 1.16 for mature and H' = 1.28 for old-growth forest stands. The index reveals that species diversity was greater in old-growth stands. Maximum diversity for mature stands was calculated as H'max = 1.51 and H'max = 1.54 for old-growth stands. Both H' and H'max values are utilized to calculate evenness, which is expressed as J' = 0.77 for mature and J' = 0.83 for old-growth stands. The greater the value of J' the greater the species diversity value. Hence J' for old-growth

indicates greater species diversity. Dominance was calculated as 1-J' = 0.23 for mature and 1-J' = 0.17 for old-growth forests. As with the Berger-Parker index, the lower the 1-J' value the greater the species diversity index.

A two-tailed t-test was used to test for differences between the Shannon diversity indices for mature and old-growth stands. Results of the t-test indicated that bird species diversity was significantly greater in old-growth rather than in mature stands ($t = -9.00$, $df = 3154$, $P = 0.000$).

Table 9. Results of Margalef's, Berger-Parker, and Shannon diversity indices for bird species, genus, and family diversity in mature and old-growth Douglas-fir stands (1988-1990).

Diversity Index	Hierarchical Diversity *					
	BSD		BGD		BFD	
	M	O-G	M	O-G	M	O-G
Margalef's Index						
Dmg, diversity	4.24	4.47	3.83	4.21	1.64	1.92
Berger-Parker Index						
d, dominance	0.16	0.14	0.16	0.14	0.49	0.48
1/d, inverse of d	6.25	7.14	6.25	7.14	2.04	2.08
Shannon Index						
H', diversity	1.16	1.28	1.15	1.27	0.72	0.70
H'max, maximum H'	1.51	1.54	1.46	1.52	1.11	1.18
J', evenness using H'	0.77	0.83	0.79	0.84	0.64	0.59
1- J', dominance using H'	0.23	0.17	0.21	0.16	0.36	0.41

* BSD = Bird Species Diversity, BGD = Bird Genus Diversity, BFD = Bird Family Diversity. M = Mature and O-G = Old-Growth.

Bird genus diversity, measured by combining bird genus abundance and richness, was found to be greater in old-growth than in mature Douglas-fir stands (Table 9). Calculations for diversity indices were based on the total number of bird genera and the total number of individuals per genus recorded during the three year study in mature and old-growth stands. Margalef's diversity index was estimated as Dmg = 3.83 and Dmg = 4.21 for mature and old-growth stands, respectively. The Berger-Parker diversity index calculated for mature stands was d = 0.16 and for old-growth stands was d = 0.14. The reciprocal of the Berger-Parker index was 1/d = 6.25 for mature and 1/d = 7.14 for old-growth stands. The Berger-Parker index for genus diversity was the same as the species diversity index presented above.

The Shannon diversity index was estimated as H' = 1.15 for mature and H' = 1.27 for old-growth forest stands. The index reveals that genus diversity was greater in old-growth stands. Maximum diversity for mature stands was calculated as H'max = 1.46 and H'max = 1.52 for old-growth stands. Evenness was calculated as J' = 0.79 for mature and J' = 0.84 for old-growth stands. Therefore, J' indicates greater species diversity in old-growth stands. Dominance was calculated as 1-J' = 0.21 for mature and 1-J' = 0.16 for old-growth forests.

A two-tailed t-test was used to test for differences between the Shannon diversity indices for mature and old-growth stands. Results of the t-test indicated that bird genus diversity was significantly greater in old-growth rather than in mature stands ($t = -7.62$, $df = 2680$, $P = 0.000$).

Bird family diversity, measured by combining the abundance and richness of bird families, was found to be similar in old-growth and mature Douglas-fir stands. Calculations for diversity indices were based on the total number of bird families and the total number of individuals per family recorded during the three year study in mature and old-growth stands. Margalef's diversity index was estimated as Dmg = 1.64 and Dmg = 1.92 for mature and old-growth stands, respectively. The Berger-Parker diversity index calculated for mature stands was d = 0.49 and for old-growth stands was d = 0.48. The reciprocal of the Berger-Parker index was 1/d = 2.04 for mature and 1/d = 2.08 for old-growth stands.

The Shannon diversity index was estimated as H' = 0.72 for mature and H' = .70 for old-growth forest stands. Maximum diversity for mature stands was calculated as H'max = 1.11 and H'max = 1.18 for old-growth stands. Evenness was calculated as J' = 0.64 for mature and J' = 0.59 for old-growth stands. Dominance was calculated as 1-J' = 0.36 for mature and 1-J' = 0.41 for old-growth forests (Table 9).

A two-tailed t-test was used to test for differences between the Shannon diversity indices for mature and old-growth stands. Results of the t-test indicate that there was no significant difference in bird family diversity between mature and old-growth Douglas-fir stands ($t = 0.98$, $df = 3182$, $P = 0.327$).

Foraging Guilds

Calculations for all diversity indices were based on the total number of bird species and individuals in each foraging guild recorded during the three year study in mature and old-growth stands. The total number of individual birds compiled by foraging guilds was greater in old-growth stands (Table 10). The three measures used to estimate bird foraging guild diversity provided differing estimates of relative diversity for mature and old-growth stands. However, the statistical test, calculated for the Shannon diversity index, indicated a greater diversity of foraging guilds in old-growth stands. Margalef's diversity index was estimated as Dmg = 0.41 and Dmg = 0.39 for mature and old-growth stands, respectively. The Berger-Parker diversity index calculated for mature stands was d = 0.58 and for old-growth stands was d = 0.48. The reciprocal of the Berger-Parker index was 1/d = 1.72 for mature and 1/d = 2.08 for old-growth stands.

The Shannon diversity index was estimated as H' = 0.43 for mature and H' = 0.46 for old-growth forest stands. Maximum diversity for mature stands was calculated as H'max = 0.60 and H'max = 0.60 for old-growth stands. Evenness was calculated as J' = 0.71 for mature and J' = .76 for old-growth stands. Dominance was calculated as 1-J' = 0.28 for mature and 1-J' = 0.24 for old-growth forests (Table 11).

A two-tailed t-test was used to test for differences between the Shannon diversity indices for mature and old-growth stands. Results of the t-test indicated that bird diversity based on foraging guilds was significantly greater in old-growth rather than in mature stands ($t = 3.18$, $df = 3200$, $P = 0.001$).

Table 10. Total number of individual birds per stand by foraging guilds in four mature (N = 1,498) and four old-growth (N = 1,995) Douglas-fir stands (1988-1990).

Stand Number	Total Number of Individuals Per Stand Foraging Guilds *				Total Number of Individuals Per Stand Foraging Guilds				Total Number of Individuals Per Stand Foraging Guilds				Total Number of Individuals Per Stand Type (Combined Years)			
	1988				1989				1990				1988-1990			
Mature	GG	BG	FG	AF	GG	BG	FG	AF	GG	BG	FG	AF	GG	BG	FG	AF
1	36	27	64	3	29	23	55	2	22	13	50	3	87	63	169	8
2	26	10	98	1	32	18	61	0	39	15	60	1	97	43	219	2
3	52	13	81	0	48	22	74	0	37	10	82	3	137	45	237	3
4	44	18	88	1	25	14	77	0	19	11	86	5	88	43	251	6
											TOTAL	=	409	194	876	19
Old-Growth																
5	71	20	103	1	51	12	93	3	44	6	67	2	166	38	263	6
6	80	22	59	8	61	21	68	6	56	14	50	7	197	57	177	21
7	52	11	75	2	70	21	94	3	54	15	91	8	176	47	260	13
8	60	26	79	5	80	30	109	0	73	30	78	4	213	86	262	9
											TOTAL	=	752	228	966	49

* Foraging Guilds

GG = Ground Gleaner FG = Foliage Gleaner

BG = Bark Gleaner AF = Aerial Forager

Table 11. Results of Margalef's, Berger-Parker, and Shannon diversity indices for bird foraging and nesting guild diversity in mature and old-growth Douglas-fir stands (1988-1990).

Diversity Index	Guild Diversity			
	Foraging Guilds		Nesting Guilds	
	M	O-G *	M	O-G
Margalef's Index				
Dmg, diversity	0.41	0.39	0.55	0.53
Berger-Parker Index				
d, dominance	0.58	0.48	0.54	0.53
1/d, inverse of d	1.72	2.08	1.85	1.89
Shannon Index				
H', diversity	0.43	0.46	0.53	0.55
H'max, maximum H'	0.60	0.60	0.70	0.70
J', evenness using H'	0.71	0.76	0.76	0.78
1- J', dominance using H'	0.29	0.24	0.24	0.22

* M = Mature and O-G = Old-Growth.

Nesting Guilds

Calculations for all diversity indices were based on the total number of bird species and individuals in each nesting guild recorded during the three year study in mature and old-growth stands. The total number of individual birds compiled by nesting guilds was greater in old-growth stands (Table 12). However, bird diversity estimated for nesting guilds was found to be similar in old-growth and mature Douglas-fir stands. Margalef's diversity index was estimated as Dmg = 0.55 and Dmg = 0.53 for mature and old-growth

Table 12. Total number of individual birds per stand by nesting guilds in four mature (N = 1,498) and four old-growth (N = 1,995) Douglas-fir stands (1988-1990).

Stand Number	Total Number of Individuals Per Stand Nesting Guilds *					Total Number of Individuals Per Stand Nesting Guilds					Total Number of Individuals Per Stand Nesting Guilds					Total Number of Individuals Per Stand Type (Combined Years)				
	1988					1989					1990					1988-1990				
Mature	BPA	GR	SH	TR	SN	BPA	GR	SH	TR	SN	BPA	GR	SH	TR	SN	BPA	GR	SH	TR	SN
1	2	19	12	61	36	1	19	6	52	31	1	21	4	44	19	4	59	22	157	86
2	3	16	14	83	19	3	18	11	49	30	0	30	10	53	22	6	64	35	185	71
3	12	23	16	76	18	6	27	5	77	29	4	28	10	74	16	22	78	31	227	63
4	8	23	10	83	27	0	13	2	78	23	2	12	2	85	20	10	48	14	246	70
														TOTAL =		42	249	102	815	290
Old-Growth																				
5	11	22	19	109	33	3	24	7	104	21	4	24	8	74	9	18	70	34	287	63
6	8	26	17	65	55	7	29	9	73	38	5	24	4	62	32	20	79	30	200	125
7	2	20	9	92	21	5	33	13	101	36	3	35	8	97	25	10	88	30	290	82
8	7	21	18	82	34	4	25	24	114	53	5	53	9	76	44	16	99	51	272	131
														TOTAL =		64	336	145	1,049	401

* Nesting Guilds

GR = Ground Nester TR = Tree Nester

SH = Shrub Nester SN = Snag Nester

BPA = Brood Parasite

stands, respectively. The Berger- Parker diversity index calculated for mature stands was d = 0.54 and for old-growth stands was d = 0.53. The reciprocal of the Berger-Parker index was 1/d = 1.85 for mature and 1/d = 1.89 for old-growth stands.

The Shannon diversity index was estimated as H' = 0.53 for mature and H' = 0.55 for old-growth forest stands. Maximum diversity was calculated as H'max = 0.70 and H'max = 0.70 for mature and old-growth, respectively. Evenness was calculated as J' = 0.76 for mature and J' = 0.78 for old-growth stands. Dominance was calculated as 1-J' = 0.24 for mature and 1-J' = 0.22 for old-growth forests (Table 11).

A two-tailed t-test was used to test for differences between the Shannon diversity indices for mature and old-growth stands. Considering nesting guild comparisons, results of the t-test indicate that there was no significant difference in bird diversity between mature and old-growth Douglas-fir stands ($t = -1.33$, $df = 2904$, $P = 0.184$).

DISCUSSION

Bird Species Abundance

The abundance of breeding birds was found to be significantly greater in old-growth stands than in mature stands. The biological significance of these results is that old-growth stands may provide optimal habitat and mature stands may provide suitable habitat for breeding birds. Other researchers also determined a significantly greater difference of bird species abundance in old-growth stands (Bull 1978, Manuwal 1991, McClelland et al. 1979, Franklin et al. 1981, Marzluff and Lyon 1983, Moore 1991). Of the 3,493 individual birds recorded during the survey, the majority (1,995) were detected in old-growth while a smaller amount (1,498) were found in mature stands. Seven bird species, great gray owls, red-breasted nuthatches, hermit thrushes, Swainson's thrushes, warbling vireos, yellow-rumped warblers, and red crossbills, were more abundant in mature stands. Other researchers have found these species to be more abundant in old-growth stands (Bull 1978, Lundquist and Mariani 1991, Hejl and Woods 1989). The remaining 30 bird species were more abundant in old-growth stands.

Each of the four old-growth stands provided habitat for more individual birds than any of the individual mature stands. Old-growth stands exhibit a greater range in environmental heterogeneity; more habitat is available for a greater number of individual birds than in mature stands (Franklin et al.1981, Franklin and Spies 1991). Spies (1991) found that old-growth forests exhibit greater plant species diversity and occurrence than

mature stands. Greater plant species diversity and occurrence may be exploited by a greater number of birds. Greater production of organic matter and nutrient cycling in old-growth stands may help produce more abundant resources that can be taken advantage of by a greater number of birds (Franklin et al. 1981, Franklin and Spies 1991a).

Old-growth stands inventoried for birds were 100-200 years older than mature stands. As forest stands age, the spatial (horizontal and vertical variation) and temporal arrangement of vegetation becomes more diverse (Spies 1991, Spies and Franklin 1991). Canopy data from this study indicated that old-growth stands were more diverse than mature stands. Two to three canopy layers were present in the old-growth stands, while only 1-2 were present in mature stands. Multiple canopy layers may provide more foraging and nesting sites for foliage gleaning and tree nesting birds (MacArthur 1958). A greater range of tree diameters was available in the old-growth stands and may provide a more varied environment for bark gleaning birds.

Canopy closure was less in old-growth stands (20-55%) than in mature stands (60-70%). Gaps in the canopy, caused by overstory tree mortality, allow for increased sunlight penetration and more precipitation that reaches the forest floor. Such canopy gaps promote the establishment and growth of herbaceous vegetation, shrubs, and young trees, which may provide additional habitat for foraging and nesting birds. Results from Spies (1991) indicated that understory vegetation diversity increases as stands age. A greater abundance of large snags and logs were present in the old-growth stands which may provide additional resources for bark foragers, ground foragers, and ground and snag nesting birds.

Bird Species Richness

The richness of breeding birds was not significantly different between old-growth and mature Douglas-fir stands. Stand composition, function, and structure, that may have contributed to greater bird species abundance in old-growth stands, did not significantly affect bird species richness. Although some bird species were found only in mature or old-growth stands, this may be the result of a small sample size. A larger sample size may have revealed that species seemingly unique to mature also inhabited old-growth stands, and those species unique to old-growth also inhabited mature stands. Because Douglas-fir trees were the common cover type, it is understandable that similar bird species would inhabit mature and old-growth stands. Moore (1991) found the same results in her analysis of this site. This finding is consistent with other researchers in similar habitats (Hejl and Woods 1989, Raphael 1991, Hutto et al. 1992).

Of the 37 bird species recorded during the study, 32 were found in mature and 35 were found in old-growth stands. Cooper's hawks and red crossbills were found only in mature stands, while red-tailed hawks, American kestrels, Steller's jays, house wrens, and white-crowned sparrows were found exclusively in old-growth stands. The remaining species were found in both stand types.

Cooper's hawks prey on other forest birds and have short, rounded wings and a long tail for aerial maneuvers that facilitate capturing prey in flight (Bent 1937, Ehrlich et al. 1988). Foraging in mature stands may increase their hunting success rate. Red crossbills were frequently seen in flocks of 5-20 individuals flying over the study area, but

rarely landed in surveyed stands. Because this species extracts seeds from Douglas-fir and other conifer cones, it seems likely that it would inhabit both mature and old-growth stands. However, red crossbills are known to nest early in the spring and may have completed their nesting cycle prior to June which was the month the study occurred (Ehrlich et al. 1988, DeGraaf et al. 1991).

Red-tailed hawks and American kestrels prefer open forest terrain for foraging which is more abundant in the patchy structure of old-growth stands (Bent 1938, Ehrlich et al. 1988). One red-tailed hawk nest was found in an open Douglas-fir stand at the top of a live tree with a dead top. American kestrel nests were found in large diameter snags. This species is a secondary cavity nester and relies on abandoned nests excavated by woodpeckers.

Steller's jays were found only in the upper elevation old-growth stands. These stands were roughly 300 m higher in elevation than the other old-growth and mature stands. White-crowned sparrows were found to be more abundant in upper elevation old-growth stands. Because of their presence in these upper stands, these two species may have been influenced by elevation rather than old-growth characteristics. House wrens were found in only one old-growth stand. House wrens were found in this stand each year of the study and apparently represented an isolated population that nested at the head of a side drainage of Pine Creek.

Hierarchical Diversity

Bird species diversity was significantly greater in old-growth stands than in mature stands. The biological significance of these results is that breeding birds are more evenly distributed in old-growth stands than in mature stands. High evenness may be an indication that breeding birds find optimal habitat in old-growth stands and suitable habitat in mature stands. Other researchers have determined that bird species diversity was not significantly different in mature and old-growth Douglas-fir stands (Carey et al. 1991, Gilbert and Allwine 1991). Given that richness, dominance, and proportional abundance were considered in each of the tested diversity indices (Magurran 1988), and that each index indicated a higher value for old-growth, the results substantiate greater bird species diversity in old-growth stands.

The proportional distribution of the abundance of species in these stand types was the key feature for greater bird diversity in old-growth stands. This distribution was based on the greater similarity of abundance of bird species in old-growth stands compared to mature stands. The ten most abundant species in mature stands represented 83% of the total birds in this stand type. The ten most abundant species in old-growth represented 74% of the total birds in this stand type. The less common species detected in the study were more abundant and more proportionately represented in old-growth stands.

Although some bird species were found only in mature or old-growth stands, other species were found in both stand types. The great gray owl, red-breasted nuthatch, hermit thrush, Swainson's thrush, warbling vireo, and yellow-rumped warbler were more

abundant in mature stands. Bull (1978) found great gray owls to be more common in old-growth habitats. In western Montana, Hejl and Woods (1989) found that the red-breasted nuthatch was more common in mature stands, but found that the hermit and Swainson's thrush were more abundant in old-growth stands. They also felt that the warbling vireo and yellow-rumped warbler were equally common in both stand types.

The American robin, chipping sparrow, Clark's nutcracker, Hammond's flycatcher, hairy woodpecker, Lincoln's sparrow, northern flicker, three-toed woodpecker, and Williamson's sapsucker were more abundant in old-growth stands. Moore (1991) found that American robins and chipping sparrows were significantly associated with old-growth Douglas-fir stands. Other researchers have found that the Hammond's flycatcher, hairy woodpecker, Lincoln's sparrow, northern flicker, three-toed woodpecker, and Williamson's sapsucker were more abundant in old-growth Douglas-fir stands (Bull 1978, McClelland 1977, Hejl and Woods 1989, Manuwal 1991, Lundquist and Mariani 1991).

Bird species diversity is an expression of community structure (Pianka 1983). The greater range and abundance of resources that were available in the inventoried old-growth stands may provide breeding birds with more habitats to exploit. Competition, predation, food webs, and niche divisions among birds are more complex in communities with high species diversity (MacArthur 1955). Ecological niches may be smaller in old-growth compared to those found in mature stands and may be the reason for higher species diversity (Pianka 1983).

When diversity was examined at the genus level, bird genus diversity was found to be significantly greater in old-growth stands. All of the diversity indices used for genus level analysis revealed a higher value for old-growth stands. However, species and genus level comparisons were very similar. The 37 species analyzed for bird species diversity represented 34 different genera examined for bird genus diversity. Therefore, at this level of taxonomic comparison, the results for genus and species comparisons were essentially the same.

Six bird species belonged to three different genera. Cooper's hawks and sharp-shinned hawks are in the genus *Accipiter,* hairy woodpeckers and three-toed woodpeckers are in the genus *Picoides,* and hermit thrushes and Swainson's thrushes are in the genus *Catharus.* All of the remaining species represented one genus each and were treated similarly as they were at the species level. Cooper's hawks were found only in mature stands. Sharp-shinned hawks were found in mature and old-growth stands. Species in this genus may be better suited to foraging in mature stands. Their success rate in capturing bird prey by aerial pursuit may be greater in this stand type. Cooper's and sharp-shinned hawks may partition resources by foraging on different bird species and nesting in different microsites (Bent 1937, Ehrlich et al. 1988, DeGraaf et al. 1991).

Hairy woodpeckers and three-toed woodpeckers were more abundant in old-growth than in mature stands. Foraging and nesting sites available in old-growth stands were more abundant for species in this genus . Both rely on logs and snags for foraging sites, and snags for cavity nesting sites (Bull 1978, McClelland 1977, Hejl and Woods 1989, Manuwal 1991, Lundquist and Mariani 1991). The variety and abundance of logs

and snags were greater in the old-growth stands inventoried in the study. Resource partitioning may enable these two species to occupy similar habitats. Ten hairy woodpecker nests were found during the study and all were in hard snags averaging 33 cm in diameter. Nine three-toed woodpecker nests were discovered during the study and all were found in hard snags averaging 28 cm in diameter (Sparks 1989 and 1990, Moore 1991).

Hermit and Swainson's thrushes were more abundant in mature stands than in old-growth stands. Mature stands may provide more resource opportunities for hermit and Swainson's thrushes. Resources appeared to be partitioned by different behavioral strategies in foraging and nesting by these two species. Hermit thrushes forage and nest on the ground; Swainson's thrushes forage mainly by gleaning invertebrates from foliage and branches and nests in shrubs or small conifers (Ehrlich et al. 1988, DeGraaf et al. 1991).

The diversity of birds based on family level taxonomy was not significantly different between mature and old-growth stands. At the family level, breeding birds may find an equal amount of optimal and/or suitable habitat in mature and old-growth stands. The proportional distribution of the abundance of species at the family level was similar in mature and old-growth stands. This was the reason that there was no significant difference between stand types.

Fifteen bird families were recorded in the study area. All of the bird families were found in old-growth, but only thirteen families were found in mature stands. Birds in the families Falconidae (American kestrel) and Troglodytidae (house wren) were not found in

mature stands. These two families represented less than 1% of the total abundance of birds in old-growth stands. The families Accipitridae (Cooper's and sharp-shinned hawks), Strigidae (great gray owl), Sittidae (red-breasted nuthatch), and Vireonidae (warbling vireo) were more abundant in mature stands. Species in the remaining families were more abundant in old-growth forests, especially Phasianidae (blue grouse), Picidae (Williamson's sapsuckers, hairy woodpeckers, three-toed woodpeckers, and northern flickers), and Tyranidae (Hammond's flycatcher).

Two of the largest families, Muscicapidae and Emberizidae, represented 66% of the total abundance of birds in the study area. Species in the family Muscicapidae and Emberizidae comprised 17% and 49%, respectively, of the individual birds found in mature stands. These two families comprised 18% and 48%, respectively, of the individual birds found in old-growth stands.

Foraging Guilds

Bird species diversity considered by foraging guild was significantly greater in old-growth stands. Breeding birds may find optimal foraging habitat in old-growth stands and suitable foraging habitat in mature stands. The proportional distribution of aerial foragers, bark gleaners, foliage gleaners, and ground gleaners was more similar in old-growth stands and therefore equated to a greater species diversity index. Bird abundance in each foraging guild was greater in old-growth stands. However, bark and foliage gleaners were proportionately more abundant in mature stands and aerial foragers and ground gleaners were more abundant in old-growth stands.

Seventy-two percent of all aerial foragers recorded during the study were detected in old-growth stands. Huff and Raley (1991) also found that aerial foragers reached their highest abundance in old-growth Douglas-fir stands. Except for Cooper's and sharp-shinned hawks that may benefit from closed forest canopies while pursuing prey, gaps in the canopy, provided in old-growth stands, may benefit other aerial foragers in capturing prey. Red-tailed hawks, American kestrels, great gray owls, Hammond's flycatchers, and Townsend's solitaires tend to forage along forest edges provided by canopy gaps which facilitates the capture of prey species (Ehrlich et al. 1988, DeGraaf et al. 1991). In particular, the Hammond's flycatcher and Townsend's solitaire were repeatedly seen foraging along edges created by canopy gaps.

Sixty-five percent of all ground gleaners were recorded in old-growth stands. Various sized canopy gaps and a greater abundance of logs, snags, and canopy layers in this stand type may have provided more foraging habitat for ground gleaning bird species. The American robin, chipping sparrow, Lincoln's sparrow, northern flicker, Steller's jay, house wren, and Cassin's finch were seen foraging within the canopy gaps associated with old-growth stands. Dark-eyed juncos were very common in mature and old-growth stands and were seen foraging under dense and open canopy conditions.

Although bark gleaners were more abundant in old-growth stands, they were proportionately more abundant in mature stands. Huff and Raley (1991) indicated that bark gleaners were more abundant in old-growth stands in Oregon and Washington. Mature stands provided one or two canopy layers and a range of tree diameters, but lacked such stand attributes as canopy gaps, logs, and snags found in old-growth stands.

Because of these deficiencies, aerial and ground foraging species were less abundant, which proportionately increased species that forage on the trunks and foliage of trees. Red-breasted nuthatches were more common in mature stands; brown creepers were equally common in mature and old-growth stands; and Williamson's sapsuckers, hairy woodpeckers, and three-toed woodpeckers were more common in old-growth.

Foliage gleaners were more abundant in old-growth stands, but were proportionately more abundant in mature stands. Mature stands generally provided more trees per hectare than old-growth stands and may have furnished more foraging sites for foliage gleaners. Results from a study by Spies and Franklin (1991) revealed that tree densities were greater in younger (<195 years) than older (>195 years) Douglas-fir stands. Red crossbills were recorded only in mature stands. Swainson's thrushes, warbling vireos, and yellow-rumped warblers were recorded in both stand types, but were more abundant in mature stands. The pine grosbeak was found equally in both stand types. All of the other foliage gleaners, including Clark's nutcrackers, mountain chickadees, ruby-crowned kinglets, MacGillivray's warblers, western tanagers, pine siskins, and evening grosbeaks were more common in old-growth stands.

Nesting Guilds

Species diversity based on bird nesting guilds was not significantly different between mature and old-growth stands. Breeding birds may find an equal amount of optimal and/or suitable nesting habitat in mature and old-growth stands. The proportional distributions of brood parasites, ground nesters, shrub nesters, snag nesters, and tree

nesters were similar in mature and old-growth stands. However, bird abundance for each nesting guild was greater in old-growth stands.

Brood parasites were represented by the brown-headed cowbird. A similar abundance of individuals (3%) was found in mature and old-growth stands. The brown-headed cowbird is a generalist brood parasite and lays its eggs in the nests of over 240 different bird species. Open-cup nests of Neotropical migratory birds are especially vulnerable to cowbirds (Robinson et al. 1991).

Ground nesting birds were represented by five species: blue grouse, Townsend's solitaire, hermit thrush, Lincoln's sparrow, and dark-eyed junco. This group represented 17% of bird abundance in both stand types. Shrub nesters were represented by the Swainson's thrush, MacGillivray's warbler, and white-crowned sparrow. This group represented 7% of bird abundance in mature and old-growth stands.

Snag nesters were represented by nine species of birds. The American kestrel, Williamson's sapsucker, hairy woodpecker, three-toed woodpecker, northern flicker, mountain chickadee, and house wren were more abundant in old-growth stands. The red-breasted nuthatch was more abundant in mature stands and the brown creeper was similarly abundant in both stand types. Snag nesting birds were more abundant in old-growth, but their proportional abundance was nearly equal: 19% in mature and 20% in old-growth stands. Other studies have shown that snag nesting birds were more abundant in old-growth (McClelland et al. 1979, Franklin et al. 1981, Marzluff and Lyon 1983).

Tree nesting birds represented over half of the birds (19 species) recorded in the study. Of these, ten species were more abundant in mature stands and nine species were more abundant in old-growth forests. The relative abundance of tree nesting birds was greater in old-growth. However, their proportional abundance was 54% and 52% in mature and old-growth stands, respectively.

As forests age from mature to old-growth, stand structure becomes more varied, trees become larger, and their mortality rate increases (Franklin et al. 1981). Dead trees provide more abundant sites for snag nesting species (McClelland 1977, Franklin et al. 1981). Canopy gaps increase sites for ground nesting birds. Shrubs and small conifers grow in the gaps and increase the availability of sites for shrub nesting species (Franklin and Spies 1991a, Spies and Franklin 1991). As conifers mature they add to the vertical structure of stands, produce multilayered canopies, and increase the amount of sites for tree nesting birds.

INTERPRETATIONS

The results of this study suggest that bird species abundance, bird species diversity, bird genus diversity, and bird foraging guild diversity are greater in old-growth than in mature Douglas-fir stands. However, bird species richness, bird family diversity, and bird nesting guild diversity were similar in mature and old-growth stands. Mature and old-growth forests are merely different temporal stages of forest succession exhibiting different levels of composition, function, and structure. Given the high proportion of forest fragmentation in this portion of the Bridger Range, resulting primarily from timber harvest, both stand types are important habitats for breeding bird communities.

Currently, the Forest Service is moving towards "ecosystem management" that blends the ecological, economical, and social attributes of forest landscapes. The agency has the opportunity, under ecosystem management guidelines, to provide local economies with goods and services while maintaining the ecological integrity of forest environments. Because of the high level of forest fragmentation in this portion of the Bridger Range, old-growth forests should be conserved and mature stands should be managed to replace old-growth stands. Similar recommendations for the conservation of old-growth forests have been proposed in other breeding bird research (Thomas et al. 1988, Hejl and Woods 1989).

Some researchers suggest that old-growth replacement stands can not be achieved with silvicultural techniques (Thomas et al. 1988). They recommend that mature stands be selected for old-growth replacement and allowed to develop under natural conditions.

However, Franklin and Spies (1991b) suggest that old-growth stands could theoretically develop following human or natural disturbance since they are defined by composition, function, and structure and not by origin. These researchers hypothesize that silvicultural techniques emphasizing multi-aged and multi-sized stands through partial cutting could create old-growth stand conditions.

Vegetative management should also emphasize the protection of large tracts of mature and old-growth forests in a wide range of cover types to maximize and conserve bird species diversity (McClelland et al. 1979, Franklin et al. 1981). Stands should not be selected randomly from the timber data base and assigned protection. Instead, field verification of stand conditions should be made prior to selecting and retaining mature and old-growth forests (Sparks 1990). Rare bird species and suites of bird species inhabiting mature and old-growth will have a greater potential for population viability if stands are managed accordingly.

The conservation of Neotropical migratory landbirds and resident birds will be facilitated by retaining, protecting, and managing young, mature and old-growth stands on a landscape level (Thompson et al. 1991). Montana Partners in Flight has developed a bird species priority list for forest habitats (Montana Partners in Flight 1997). This list includes species such as the northern goshawk, great gray owl, Williamson's sapsucker, red-naped sapsucker, olive-sided flycatcher, Hammond's flycatcher, brown creeper, and MacGillivray's warbler, all of which were detected in the Bridger Range study area. Forest management that emphasizes the preservation of old-growth stands and applies the

silvicultural techniques listed above will promote the conservation of breeding bird communities in this area.

The study was limited to the area located inside the boundary of the Pine-Slushman Timber Sale. Although the stands selected for the study followed the Gallatin National Forest definition for mature and old-growth forests, stands located outside the sale area boundary may have better represented these stand types. Because of this limitation, stands of various sizes were selected for breeding bird inventories. Comparing breeding bird data in stands of varying sizes may have biased the results. The study area has been extensively fragmented by timber harvest that may have affected the breeding bird community structure. Consequently, the results of this study may not apply to other Douglas-fir communities on the Forest.

The methods utilized, the collection of three years of data, and my knowledge of breeding birds in Douglas-fir forests contributed to the strengths of the study. The consistency of studying breeding birds during June in each of the survey years, inventorying the same number of mature and old-growth stands, and applying the methods equally to each stand gave added value to the results of the study. Collecting three years of breeding bird information increased the amount of data that was collected for the study. This may have enhanced the accuracy of the results of the project. My knowledge of breeding birds and their identification reduced the error and increased the accuracy of the data applied to the results of the study.

Future research on breeding bird communities in Douglas-fir forests should emphasize species specific analysis, studies in other vegetative age classes, and studies in landscapes that are not fragmented by timber sales. Species specific analysis may help identify birds that are mature or old-growth obligates or birds that are more common in theses stand types. Identification of such species will facilitate their conservation. Research in different vegetative age classes may help identify the structural attributes important to breeding birds. Studies analyzing the effects of different timber harvesting methods, the effects of prescribed and natural fire, and the progression of forest succession under these different disturbances may contribute to the conservation of breeding birds. Forested areas that are not fragmented by timber harvest are becoming increasingly uncommon. Breeding bird studies in unfragmented forest landscapes may reveal different results in species diversity than studies in fragmented forest landscapes.

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