AN ABSTRACT OF THE DISSERTATION OF

A. Kari Stuart-Smith for the degree of Doctor of Philosophy in Forest Science, presented on December 4, 2001. Title: Songbird Communities in Burned and Logged Stands with Variable Tree Retention in the Canadian Rocky Mountains

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John P. Hayes

By emulating natural disturbances such as wildfire, managers hope to maintain biodiversity in managed forests. Leaving residual (live) trees in harvested areas is key to this strategy. However, the effectiveness of this approach is unknown. I surveyed songbirds in 176 stands in the Rocky Mountains of southeastern British Columbia, Canada, that had been logged or burned by wildfire. Stands varied in time-since-disturbance from 5-45 yr. and in residual tree density from 0-216 conifer overstory, 0-268 conifer understory, and 0-35 broadleaf trees/ha. In 28 of these stands, artificial and natural nests were used to examine nest predation.

Logged and burned stands had similar dominant species, evenness, and diversity (Simpson's index) of birds, but logged stands had higher richness and abundance. Of 26 species analyzed, 20 had similar or greater abundance in logged stands; 6 had greater abundance in burned stands. Differences in songbird communities were likely related to differences in vegetation. As a result of non-intensive logging practices, logged stands had greater shrub cover, shrub richness, broadleaf tree basal area, and more vegetation layers, but fewer regenerating trees, snags, and down wood than burned stands. As time-since-disturbance increased, bird communities in the two disturbance types became more similar at higher elevations, but not at lower elevations.

Residual broadleaf and conifer understory tree density positively influenced songbird richness and abundance. Abundance of individual bird species was positively and negatively associated with residual trees. There was no strong or consistent evidence that depredation of nests of ground- and shrub-nesting songbirds increased with residual tree density. Depredation of artificial nests increased with residual tree density in logged stands in one of two years, but not in burned stands. Depredation was higher for artificial than natural nests.

Retaining residual trees in managed stands can enhance richness and abundance of songbirds without increasing nest predation. The range of densities in this study provided

good habitat for most early seral songbirds, but higher densities of overstory trees and snags are needed to provide good habitat for some species. Logging practices that reduce broadleaf trees, shrub cover, or residual conifer understory trees may reduce songbird richness and abundance.

SONGBIRD COMMUNITIES IN BURNED AND LOGGED STANDS WITH VARIABLE TREE RETENTION IN THE CANADIAN ROCKY MOUNTAINS

by:
A. Kari Stuart-Smith

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I understand that my dissertation will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes release of my dissertation to any reader upon request.

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A. Kari Stuart-Smith, Author

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SONGBIRD COMMUNITIES IN BURNED AND LOGGED STANDS WITH VARIABLE TREE RETENTION IN THE CANADIAN ROCKY MOUNTAINS

INTRODUCTION

In recent years, the goal of many natural resource management agencies in North America has broadened from sustaining production of commodities to sustaining the ecosystems that produce those commodities (Haynes et al. 1996, Manley et al. 1995, BC Environment 1995, Kaufmann et al. 1994). Sustaining ecosystems can be interpreted as maintaining native species, processes and components, and long-term productivity (Cissel et al. 1998). There are many different visions of what ecosystem management entails (e.g., Franklin 1997, Haynes et al. 1996, Christensen et al. 1996, Wilcove and Blair 1995, Grumbine 1994), and it is perhaps best described by a cluster of concepts (Lertzman et al. 1998) rather than with one discrete definition. Common themes include recognition that ecosystems operate over a broad range of temporal and spatial scales and have a hierarchical and dynamic nature, recognition that humans are ecosystem components and ecosystems provide a broad range of human values, an understanding of the importance of monitoring and adaptive management, and the primacy of maintaining ecological integrity (Lertzman et al. 1998, Christensen et al. 1996, Grumbine 1994). Key among these is the recognition that successful ecosystem management must be based on an understanding of the dynamic character of ecosystems and the critical role that disturbance plays in ecosystem structure and function (Christensen et al. 1996).

Disturbance is commonly defined as any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment (Pickett and White 1985). Natural disturbances occur at many temporal and spatial scales and include fire, windstorms, floods, insects, disease, floods, and volcanic eruptions. These disturbances create a mosaic of successional patches across landscapes (Pickett and White 1985). An extensive literature supports the hypothesis that natural disturbance is fundamental to structure and function of forest ecosystems (Attiwill 1994), and there is evidence that native species have adapted to disturbance regimes (e.g., Bunnell 1995). Characteristics of ecosystems where natural disturbance has been removed provide evidence of this. For example, the exclusion of low-intensity, surface fires from the ponderosa pine (*Pinus ponderosa*) forests of western interior North America has drastically altered forest ecosystem structure and function, such that catastrophic wildfire and insect outbreaks now threaten the ecosystem and many endemic wildlife species (Fule et al. 1997).

The Natural Disturbance Approach to Resource Management

Based in part on the increasing awareness of the importance of disturbance in ecosystems, the concept of natural variability has emerged as a paradigm for ecosystem management in western North America (Morgan et al 1994, Cissel et al. 1994, Swanson et al. 1993). Natural variability (sometimes called the historic range of variability) refers to variability in the composition, structure, and dynamics of ecosystems before European settlement (Swanson et al. 1993). The concept relies on two ideas: that past conditions and processes provide context and guidance for management of ecological systems today, and that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems (Landres et al. 1999). The natural disturbance approach rests on the premise that native species have persisted through or adapted to the disturbance events of recent millennia (Bunnell 1995, Swanson et al. 1993, Hunter 1993). Thus, the more that managed ecosystems resemble those created through natural disturbance, the greater the likelihood that native species and ecological processes will be maintained (Swanson et al. 1993).

The use of the natural variability concept is not an attempt to return landscapes to wilderness states or return them to a single, pre-existing condition, but rather, to meet ecological objectives by bringing landscapes within their natural range (Swanson et al. 1993). Recognizing that we have incomplete knowledge of species and functions within ecosystems to manage on a species-by-species basis, the natural variability approach assumes that maintaining the patterns and processes of natural disturbance, and thus a range of habitat types similar to historic distributions, will provide for viable populations of most species. Thus, it is often referred to as a “coarse-filter” strategy (Hunter 1990). Unlike the coarse-filter strategy advocated by the Nature Conservancy (Hunter 1991), however, it focuses on disturbance regimes which create ecological communities, rather than on the communities themselves.

The natural disturbance approach provides an ecological baseline against which to evaluate ecosystem change associated with current conditions and future alternatives (Morgan et al. 1994, Kaufmann et al. 1994, Swanson et al. 1993). The risks and probabilities of changes in ecosystems are likely to be related to the magnitude and direction of departures from the historical range of variability (Morgan et al. 1994). Managers may not want to target natural variability as a management objective, however, because it does not account for the influences humans have had on their environment (post-European settlement), nor all the values that humans want to produce from their environment (Morgan et al. 1994).

The natural variability approach is not without limitations. Determining the range of natural variability is often hampered by a lack of historical data and difficulties in interpreting the historical record, and selecting the appropriate time period as a reference can be challenging (Wimberly et al. 2000, Cissel et al. 1998, Morgan et al. 1994). Returning ecosystems to within their range of natural variability can be difficult where human activities have drastically altered ecosystems, or where disturbances were infrequent and catastrophic (Swanson et al. 1993). Critics have charged that changes in ecosystems due to exotic species, climate change, and human constructs with no natural analogue such as roads make returning to natural variability impossible or inappropriate (Swanson et al. 1993). A disturbance regime emulating natural variability may interact with these changes in current or future ecosystem condition to trigger ecosystem responses far outside the range of natural conditions (Swanson et al. 1993). Finally, components of natural disturbance regimes, such as very large (> 100,000 ha) wildfires, may be viewed as unacceptable by many segments of society (Cissel et al.1998, Hunter 1993).

Despite these limitations, the natural disturbance approach provides an alternative to other approaches to forest management such as the sustained yield model traditionally followed by foresters, or the reserve, corridor and matrix concept often advocated by conservation biologists (Noss and Cooperrider 1994). In the United States, the implementation of ecosystem management by natural resource agencies relies heavily on the concept of natural range of variability (Kaufmann et al. 1994) or reference variability (Manley et al.1995) in defining sustainable target conditions for managed lands (but see Espy and Babbitt 1994). Examples of its diverse application range from the planned flooding of the Colorado River from Glen Canyon dam (Patten et al. 2001), the development of recovery plans for freshwater habitats of anadromous salmonids (Reeves et al. 1995), to the development of landscape plans for forest management (Cissel et al. 1998, 1999). The latter, the use of the natural disturbance approach for forest management, is the focus here.

Natural Disturbance and Forest Management

The concept of using natural disturbance patterns as a guide for forest management is currently being explored throughout boreal and temperate forests in North America and Scandinavia (e.g., Bergeron et al. 1999, Angelstam 1998, Cissel et al. 1998, Johnson et al. 1998, Fule et al. 1997, Stuart-Smith and Hebert 1996, BC Environment 1995) as well as internationally through the Santiago Declaration of 1995.

In forests, the main agents of disturbance include fire, insects, wind storms, ice storms, landslides, and floods. Disturbance regimes can be characterized on three axis: frequency, size, and intensity (Pickett and White 1985), each of which can be quantified with frequency or probability distributions. These distributions can serve as guides for forest management in three basic ways (Hunter 1993). First, the frequency, or range of disturbance return intervals, could be emulated with a similar range of rotation ages and through amounts of each seral stage in the landscape. Second, the size and spatial distribution of disturbances could be matched by a similar size distribution of harvest openings and their spatial distribution on the landscape. Third, the range in intensity or severity of disturbances could be emulated through a range of harvest intensities, created by leaving variable amounts of live (residual) trees and dead wood, and variable degrees of soil disturbance.

In this dissertation I focus on disturbance severity, examining the specific disturbances of wildfire and timber harvest. Fire severity depends on many factors, including weather conditions, vegetation type, fuel condition, fuel load, topography, and the locations of wetlands and waterbodies (Williams and Rothermel 1992, Rowe and Scotter 1973). The severity of a fire may influence many ecological components, including soil nutrients, soil organic matter, dead wood, seed banks, and the number of live trees remaining. These live, or residual trees, can provide an index to the severity of the fire. Low severity fires, such as those that typically burned western ponderosa pine forests at frequent intervals killed few large diameter pines (e.g., Fule et al. 1997). Even in areas characterized by widespread, severe fires, such as the boreal forest (Weber and Flannigan 1997) or the northern Rocky Mountains (Van Wagner 1995), wildfires seldom kill all the trees within their boundaries, and clumps, islands and single live trees often remain. For example, estimates of percentages of live trees remaining following wildfire range from 0.6–26 % in the northern Rocky Mountains (Stuart-Smith and Hendry 1998), and 0–5.2 % in the boreal forest (Eberhart and Woodard 1987).

Residual trees are thought to play an important role in the ecology of young forests. In recently burned areas, they may provide seed sources for natural reforestation (Eberhart and Woodard 1987), or refugia for organisms, allowing some individuals to survive the fire and an area for recolonization (Franklin et al. 1997). They create structural complexity in the regenerating stand by providing large trees, variability in tree size, and a source of snags, forest gaps, and down wood. Structural complexity is associated with several ecological properties, including productivity and biodiversity (Hansen et al. 1991). In harvested stands, residual trees provide below-ground live roots which have been reported to influence spatial patterns of soil invertebrates and physical characteristics of soils (Torgerson et al. 1995). Other hypothesized benefits of retaining residual trees in managed forests include maintenance of tight nutrient cycles, refugia and inocula for nonvagile mycorrhizae and nitrogen-fixing bacteria, beneficial predator-prey relationships among forest invertebrates, habitats for vascular plants and vertebrates that require either structural complexity and/or late-seral stands, and dispersal opportunities for species that avoid forest openings (Franklin et al. 1997, Hansen et al. 1995a).

In recognition of these potential benefits, variable retention, in which variable densities of residual trees and snags are left within harvested areas, is emerging as a major strategy for integrating ecological and economic objectives for forest management in temperate forests (Franklin et al. 1997). However, this approach remains largely untested and many questions remain; will leaving residual trees make young managed stands more similar to young naturally-disturbed stands, thereby helping to maintain ecological integrity in managed forests? To achieve this: how many trees should be retained, what types of trees should be retained, and in what pattern should they be retained? To answer these questions, and in order to test the natural disturbance approach, studies of residual tree patterns in naturally disturbed stands, studies on the influence of residual trees on ecosystem structure and function, and comparisons between managed stands and naturally disturbed stands are badly needed. Given the obvious differences between wildfire and harvested stands which cannot be mitigated (the creation of snags by wildfire and the removal of tree boles by logging as one example, or the creation of roads by logging as another) differences in the pathways of recovery are also very important questions, and whether initial differences between fire and logging diminish through time.

Such studies have only recently begun to be conducted. Carleton and MacLellan (1994) found significant differences in the vegetation of boreal forests post-wildfire versus post-logging, including evidence of a conversion from conifer dominance, mostly *Picea mariana*, to dominance by *Populus* spp. in stands that had been mechanically skidded. Ehnes and Shay (1995) also found different patterns of post-disturbance recovery in the vegetation in logged versus burned stands in the boreal forest. Lee et al. (1999), in a comprehensive study that included vegetation, soils, birds, and mammals, also found significant differences between post-wildfire and post-logging stands in the boreal mixedwood forest, but reported that most differences diminished through time (0-28 yr.), with the exception of organic soil carbon.

Birds and Forest Management

For songbirds, the focus of this dissertation, the pattern of research has been similar. Many studies address the effects of wildfire on birds (e.g., Dieni and Anderson 1999, Hutto 1995, Wooller and Calver 1988, Raphael et al. 1987, Apfelbaum and Haney 1981, Taylor and Barmore 1980, Niemi 1978, Brock and Lynch 1970, Hagar 1960) and the effects of forest harvesting on birds (e.g., Costello et al. 2000, Hagan et al. 1997, Thompson et al. 1992, Crawford et al. 1981). Using naturally disturbed stands as a 'control' for harvested stands represents a substantial paradigm shift from previous research. Until recently, the effects of timber harvesting on birds were almost always evaluated by a comparison of post-harvest stands to mature or old stands, or before and after studies comparing how much community composition changed in response to harvesting (Hutto 1995, Hejl et al. 1995, Hutto et al. 1993). The treatment that best mitigated the effect of harvest, or produced the least change, was generally viewed as the best alternative.

Recently, several studies have compared the influence of wildfire and logging on birds. Most of these were conducted in the boreal forest (Stuart-Smith et al. In Press, Schieck and Hobson 2000, Hobson and Schieck 1999, Imbeau et al. 1999), with one occurring in the hardwood forests of Minnesota (Schulte and Niemi 1998) and one in the mixed conifer forests of the northern Rockies (Hutto 1995). Only one of these studies (Schieck and Hobson 2000), however, examined the influence of disturbance severity, as assessed through numbers of residual trees, in addition to disturbance type.

Residual trees, because they increase the structural complexity of stands, should strongly influence the bird community. Several classic studies have documented fundamental relationships between birds and habitat structure (Roth 1976, Willson 1974, MacArthur and

MacArthur 1961). MacArthur and MacArthur (1961) showed that an increase in foliage height diversity was associated with an increase in bird species diversity, while Roth (1976) was able to relate bird species diversity to the heterogeneity, or horizontal patchiness of the vegetation. Willson's (1974) study showed that the addition of trees in particular has a major impact on the addition of bird species. Her study of a series of increasingly structurally complex habitat types, from old fields to woodlands, showed that development of a good ground layer cover results in the addition of one guild of birds, development of the shrub layer may add any of four other guilds, and development of the tree layer often results in the addition of seven to nine more guilds, while one guild is lost (Willson 1974). The greater size and more complex structure of trees provides a greater diversity of foraging and nesting sites than shrubs or grasses.

That birds are strongly related to the structure of vegetation is also evidenced by results from studies that have compared bird communities among harvested areas with different silvicultural treatments. Clearcuts with patches of trees left within them (Merrill et al. 1998, Lindenmayer and Franklin 1997, Siep and Parker 1997) and partial cuts (Norton and Hannon 1997, Hagan et al. 1997, Crawford et al. 1981) provide habitat for more or different species than clearcuts do. Few studies have examined the influence of variable densities of residual trees. Those that have, report similar results (Schieck et al. 2000), although thresholds in the response of some species may be present (Hansen et al. 1995b).

However, few studies have examined the reproductive success of birds breeding in stands with residual trees (Dugay et al. 2001, King and DeGraaf 2000). Abundance is not correlated with reproductive success in all habitat types, so abundance cannot be assumed to reflect habitat quality in all cases (Vickery et al. 1992a, Van Horne 1983). Predation is the main cause of nest failure in most temperate landbird communities, accounting for an average of 80 % of the nest losses of open-cup nesting birds (Martin 1993b, Martin 1992, Ricklefs 1969). It is thought to be a powerful force shaping many aspects of avian reproductive ecology and life history (Sieving and Willson 1998, Martin 1993a, Martin 1988, Slagsvold 1982).

Residual trees could increase predation on ground and shrub-nesting birds by providing perches for avian predators, enabling them to be more successful predators (Yahner and Wright 1985), or by providing habitat or facilitating travel through harvested areas for nest predators such as red squirrels (*Tamiasciurus hudsonicus)* (Tittler and Hannon 2000). Only two studies have examined predation in relation to residual tree density (Tittler and Hannon 2000, Vega 1993), reaching opposite conclusions. Since green-tree retention is increasingly replacing clear-cutting, if predation is higher in stands with residual trees, some bird species may suffer reduced nesting success and possibly population declines. To determine if this is in fact the case, rigorous experimental studies comparing rates of nest predation in stands with variable amounts of residual trees and comparing managed and naturally disturbed stands are needed.

Objectives and Approach

The main objective of this dissertation was to compare the abundance, richness, community structure, and nest predation of songbird communities in post-harvest and post-wildfire stands of similar time-since-disturbance, in relation to the density and type of residual trees. I tested six specific hypotheses:

1. Songbird abundance, richness, community structure, and abundance of individual species do not differ between post-harvest and post-wildfire stands.
2. Densities of conifer overstory trees, conifer understory trees, and broadleaf trees influence the abundance of individual species, species richness, and total abundance.
3. The similarity of songbird communities in logged and burned stands increases as time-since-disturbance increases.
4. The amount of predation on nests of ground and shrub-nesting songbirds is positively related to the density of residual overstory conifer trees in a stand.
5. There is no difference in the amount of nest predation between logged and burned stands of similar time-since-disturbance.
6. The amount of nest predation on artificial nests is similar to that on natural nests.

The first three hypotheses are addressed in Chapter 2, the following three in Chapter 3. Studies addressing these sorts of questions typically select a small number of stands for intensive study, carefully chosen to be relatively homogenous (e.g., Lee et al. 1999). Rather than restrict the scope of the study to a limited number of stands in this fashion, I chose to use a random stratified design. I selected 176 study stands from a pool of 750 potential stands spread over approximately 100,000 ha, covering a range of stand types and time-since-disturbance (5–45 yrs.) within the montane forest of the Rocky Mountains in south-eastern

British Columbia, Canada. Extensive studies employing random stratified designs are rare, particularly in this sort of terrain, due to logistical difficulties.

In addition to collecting data on songbirds, I also recorded all encounters with large and medium vertebrates within the entire study area. In a long-term study of vertebrate populations in the Yukon, Hochachka et al. (2000) found that encounter rates were generally an accurate reflection of variation in population size. Although the data may not be directly pertinent to this dissertation, it provides a baseline for future comparisons in the study area, and did not involve any extra cost in collecting.

The songbird community (members of the order Passeriformes, the 'perching' birds) was used as the focal community for several reasons. Passerines form the most diverse vertebrate community in the Rocky Mountains of south-eastern British Columbia, consisting of over 60 species from 20 families (Campbell et al. 2001, Campbell et al. 1997). The community as a whole includes diverse habitat associations, with individual species likely to be closely associated with elements of the vegetation (DeGraaf et al. 1998, Willson 1974, MacArthur and MacArthur 1961). Songbird communities are relatively simple and inexpensive to census during the breeding season, and large areas can be censused quickly with skilled observers. Finally, there is conservation concern over many members of the order Passeriforms, because declines of mature forest dwelling birds have been observed for some time (e.g., Terborgh 1989, Robbins et al. 1989). Although recent evidence shows many of these declines to be primarily in species breeding in early successional habitats in northeastern North America (Franzreb and Rosenberg 1997) many species in western North America are have also showed significant long-term declines (1968-1996), including both neo-tropical migrants and residents (e.g., Olive-sided Flycatcher, Gray Jay, Pine Siskin, Wilson's Warbler, Ruby-crowned Kinglet; Campbell et al. 2001; see Appendix A for scientific names). An understanding of the ecological factors influencing habitat use among birds is important not only for providing insights into the ecological and evolutionary processes shaping life-history strategies, but also to provide critical information on which to base sound decisions in land management ensuring conservation of birds (Martin 1993a).

THE INFLUENCE OF DISTURBANCE TYPE AND RESIDUAL TREE DENSITY ON THE ABUNDANCE AND DISTRIBUTION OF BIRDS IN THE CANADIAN ROCKY MOUNTAINS

Introduction

The role of disturbance in creating and maintaining ecosystem structure and function is increasingly being recognized by ecologists (e.g., Christensen et al. 1996, Attiwill 1994, Pickett and White 1985). Defined as any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment (Pickett and White 1985), natural disturbance occurs at many temporal and spatial scales and includes fire, windstorms, floods, insects, disease, floods, landslides, and volcanic eruptions. These disturbances create a mosaic of successional patches across landscapes (Pickett and White 1985). The hypothesis that natural disturbance is fundamental to the structure and function of forest ecosystems is supported by an extensive literature (Attiwill 1994), and there is evidence that native species have adapted to disturbance regimes where they live (e.g., Bunnell 1995).

Resulting in part from this awareness of disturbance, the concept of natural variability has emerged as a paradigm for ecosystem management in western North America (Morgan et al 1994, Cissel et al. 1999, Swanson et al. 1993). The concept relies on two ideas: that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems, and that past conditions and processes provide context and guidance for management of ecological systems today (Landres et al. 1999). The application of this idea to resource management rests on the premise that native species have persisted through or adapted to the disturbance events of the Holocene (Bunnell 1995, Swanson et al. 1993, Hunter 1993). Thus, the more that managed ecosystems resemble those created through natural disturbance, the greater the likelihood that native species and ecological processes will be maintained (Swanson et al. 1993).

The concept of using natural disturbance regimes as a guide for forest management is currently being explored throughout boreal and temperate forests in North America and Scandinavia (e.g., Bergeron et al. 1999, Angelstam 1998, Cissel et al. 1999, Johnson et al. 998, Fule et al. 1997, Stuart-Smith and Hebert 1996, BC Environment 1995). Hunter (1993) and Swanson et al. (1993) identify three characteristics of disturbance regimes that could be emulated through timber harvest practices: rate of return, size and spatial distribution, and severity. Others have examined rate of return and spatial pattern (Armstrong et al. 1999, Cissel et al. 1999). Here, I focus on disturbance severity, and the specific disturbances of wildfire and timber harvest.

Wildfires vary considerably in severity, ranging from low intensity ground fires, such as those that typically burned western ponderosa pine forests at frequent intervals (Fule et al. 1997), to massive conflagrations covering thousands of hectares, such as those common in the boreal (Weber and Flannigan 1997) and northern Rocky Mountain forests (Van Wagner 1995). Even the most severe fires, however, leave residual (live) trees within their boundaries (Stuart-Smith and Hendry 1998, Eberhart and Woodard 1987). Residual trees are thought to play an important role in the ecology of young forests, providing seed sources for natural reforestation (Eberhart and Woodard 1987), and refugia for organisms, allowing some individuals to survive the fire and an area for recolonization for others (Franklin et al. 1997). Residual trees create structural complexity, associated with productivity and biodiversity (Hansen et al. 1991), by providing large trees, variability in tree size, and a source of snags, forest gaps, and down wood in young stands.

In recognition of the ecological role played by residual trees, ecologists are advocating that variable densities of live trees be left within harvested areas (Franklin et al. 1997, Hansen et al. 1995a, Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995). However, many questions regarding this practice remain; will leaving residual trees create managed stands similar to naturally-disturbed stands, thereby helping to maintain ecological integrity in managed forests? To achieve ecological integrity, how many trees should be retained, what types of trees should be retained, and in what pattern should they be retained? To answer these questions, studies are needed on residual tree patterns in naturally disturbed stands, the influence of residual trees on ecosystem structure and function, and comparisons of ecological communities in post-harvest and post-wildfire stands.

Only recently have such studies been conducted (e.g., Lee et al. 1999, Ehnes and Shay 1995, Carleton and MacLellan 1994). As social and logistical constraints prevent managers from mimicking all aspects of wildfire in managed forests (i.e. number of snags produced, total area burned at one time), understanding which aspects of wildfire have the greatest influence on ecosystem structure and function is critical. Studies comparing ecological communities in post-wildfire versus post-harvest stands are necessary to understand if or where trade-offs between emulating disturbance and producing timber can be made without compromising ecological integrity, and whether some structural attributes that can be left by harvesting can act as surrogates for those attributes that cannot. Further, if wildfire suppression and logging continue, the amount of habitat affected by wildfire will decline and that affected by logging will increase. Thus, differences in habitat created by wildfire and logging may have important implications for the populations of many species.

The main objective of this study was to compare songbird (passerine) communities in post-harvest and post-wildfire stands in relation to the density of residual trees. I tested hypotheses that 1) total abundance, richness, the abundance of individual species, and community structure do not differ between burned and logged stands, and 2) density and type of residual trees influence the abundance of individual species, as well as species richness and total abundance.

Few studies have compared the influence of wildfire and timber harvesting on birds. Of those that have, most were conducted in the boreal forest (Stuart-Smith et al. In Press, Schieck and Hobson 2000, Hobson and Schieck 1999, Imbeau et al. 1999), with one occurring in the hardwood forests of Minnesota (Schulte and Niemi 1998) and one in the mixed conifer forests of the northern Rockies (Hutto 1995). Only one of these studies (Schieck and Hobson 2000) examined the influence of disturbance severity, as assessed through numbers of residual trees, in addition to disturbance type. Residual trees, because they increase the structural complexity of forest stands, should strongly influence the bird community. Several classic studies have documented fundamental relationships between birds and habitat structure, showing species diversity to increase with the volume and vertical diversity of vegetation (Willson 1974, MacArthur and MacArthur 1961). As might be predicted from this result, harvested areas containing patches of trees (Merrill et al. 1998, Lindenmayer and Franklin 1997, Siep and Parker 1997) and partial cuts (Norton and Hannon 1997, Hagan et al. 1997, Crawford et al. 1981) generally provide habitat for a greater diversity of bird species than clearcuts do.

Only two studies have examined the influence of variable retention harvesting on birds. These report similar results to the above studies (Schieck et al. 2000), although thresholds in the response of some species may be present (Hansen et al. 1995b). Single scattered residuals provide localized resources for species such as woodpeckers, flycatchers, and raptors that forage in young stands but require large trees for perching or nesting (Schieck and Hobson 2000), whereas larger patches of residuals may retain some of the characteristics of old forest within young post-harvest stands (Siep and Parker 1997). As rotation ages are often younger than the length of time required to develop the structural features such as large diameter trees and snags that are typical of old stands, leaving these structures in cutovers may provide habitat for species dependent upon these features (Schieck and Hobson 2000).

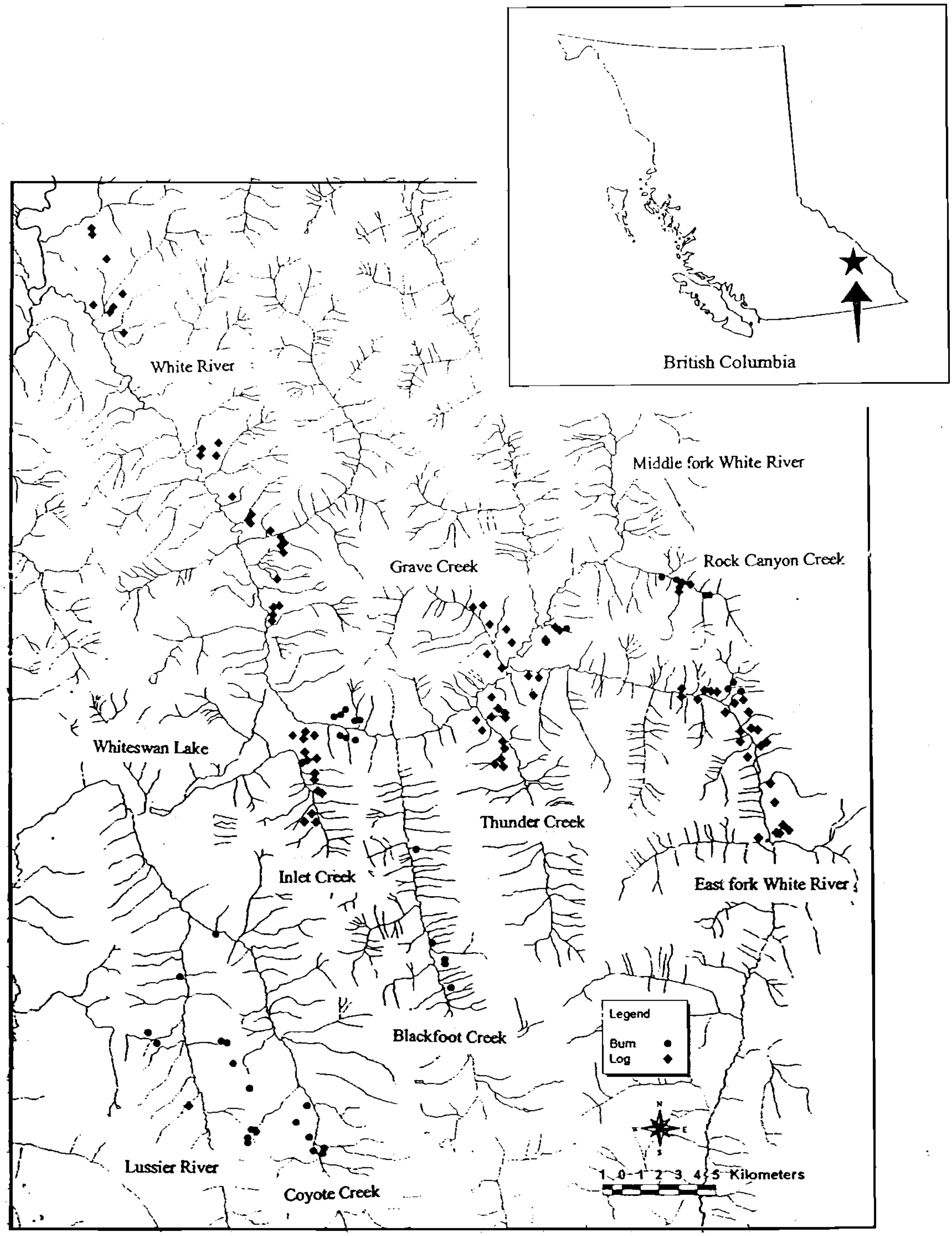
A final objective of this study was to determine whether bird communities in logged and burned stands become more similar to one another through time. Other studies have reported differences between post-harvest and post-wildfire stands to be most significant immediately following the disturbance (Lee et al. 1999, Schieck and Hobson 2000). I expected differences in community structure between the disturbance types to be manifested shortly following disturbance because of differences in numbers of snags, and because trees may establish more quickly on logged sites following planting of seedlings. These differences in habitat should decrease through time as snags fall and as vegetation becomes dominated by pole-sized trees (Hobson and Schieck 1999). Whether the communities converge through time has important management implications: if communities diverge through time, we will not be able to model bird communities in young logged stands into the future by surveying communities in mature or old stands now. Further, divergence would imply that current forest management is producing avian communities with no natural analog.

Methods

Study Area

The study was conducted in the Rocky Mountains of southeastern British Columbia, Canada, in the White, Lussier, (49°54' - 50°24' N, 115°36' -115°06' W), and Vermilion (50°56' - 51°13' N, 115°50'- 116°05' W) watersheds (Figure 2.1). The area includes forests managed for timber production and protected forests (national parks), and covers approximately 100,000 ha within the Dry Cool Montane Spruce (MSdk, hereafter MS) and the Dry Cool Engelmann Spruce-Subalpine Fir (ESSFdk, hereafter ESSF) biogeoclimatic subzones (Braumandl and Curran 1992).

Figure 2.1 Location of point count stations within the study area, Central Rocky Mountains, British Columbia, Canada. Not all point count stations are shown, because GPS positions could not be obtained for some (n=36), including those in Kootenay National Park, approximately 70 km north of the figure border.



The MS occurs from 1200 to 1650 m in elevation on south aspects and 1100 to 1550 m on north aspects and is dominated by interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), white spruce (*Picea glauca*), and western larch (*Larix occidentalis*). Extensive seral stands of lodgepole pine (*Pinus contorta* var. *latifolia*) are common due to widespread fires, and trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) are present, particularly at lower elevations. Understory vegetation is dominated by buffaloberry (*Sheperdia canadensis*), Utah honeysuckle (*Lonicera utahensis*), Sitka alder (*Alnus crispa sinuata),* common juniper (*Juniperus communis*), Oregon grape (*Mahonia aquifolium*), and pinegrass (*Calamagrostis rubescens*).

The ESSF ranges from 1650 to 2100 m on south aspects and 1550 to 2050 m on north aspects and is dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Seral stands of lodgepole pine are common, but aspen and paper birch occur rarely. False azalea (*Menziesia ferruginea*) dominates the shrub layer, with lesser amounts of black huckleberry (*Vaccinium ovalifolium*) and white-flowered rhododendron (*Rhododendron albiflorum*). The climate in both zones is characterized by warm dry summers and cold winters. Snowfall varies with elevation, increasing substantially at higher elevations in the ESSF.

Historically, stand-replacing (crown) fires have been the dominant disturbance shaping these landscapes (Van Wagner 1995). Fire suppression in the study area began in the mid-1960's, but was not effective in the early years (R. Hendry, Ministry of Forests British Columbia, pers. comm.). Three large (2,845 - 16,676 ha) wildfires occurred in the study area in 1985, and several smaller fires occurred between 1955 and 1970. Forests managed for timber production have been logged extensively since 1958.

Study Design

I randomly selected 176 point count stations in stands that were logged (logged) and those that were burned by wildfire (burned) from a pool of 750 potential stations identified from aerial photographs, digital orthophotos, and forest cover maps. This pool included all potential stations in the study area. Potential stations were initially stratified into two disturbance classes (burned and logged), three age classes (5-15, 16-30, and 31-45 yr. since disturbance), and four severity classes (0-10, 10-25, 25-50, and > 50 % cover of residual trees remaining, based on ocular estimation). Residual trees were defined as trees that survived the disturbance and were alive at the time of the study. Each potential station was defined as a circular area of at least 300 m diameter (7.07 ha), that occurred entirely within one disturbance class, was relatively homogeneous in distribution of residual trees, and was centered less than 700 m from a road or walkable trail. As most of the study area is heavily roaded, using the latter criterion excluded few potential stations. I attempted to select 7 stations in each stratum, but this was not always possible due to the fire history of the area. Most stations (140) were selected in 1997, but 36 additional stations were added in 1998 using the same random stratified design and pool of potential stations.

Bird Sampling

Birds were surveyed at each station using variable-distance point counts (Reynolds et al. 1980) three times each year between late May and early July from 1997 to 1999, between 05:30 and 09:30 h. The order that stations were surveyed was varied so that in any given year no station was surveyed at the same time each morning, and no observer surveyed the same station twice. Over the three years of the study 13 observers counted birds, including two observers that were present for two years and one that was present for all three years. Observers, most of whom were experienced birders, trained in the study area for two weeks prior to the start of counts. Hand-held recorders were used during counts to record unusual songs for later confirmation with other observers. The distance to each bird seen or heard within a 150 m radius of the center during a 12-min period was estimated during each visit. A maximum radius of 150 m was chosen as many of the sites were very open, and bird vocalizations were audible a long distance from the point center. Distance was estimated to the nearest m for birds < 20 m from the point count center, to the nearest 5 m for birds 20-65 m from the center, and to the nearest 10 m for birds 70-150 m from the center. Flags were placed at 25, 50 and 100 m from the center point to aid in distance estimation, and range finders were used to assist in determining distances to birds that were visually detected. Observers practiced distance estimation as a group for two weeks prior to the start of counts. Counts were not made during periods of wind or moderate rain.

Vegetation Sampling

At each point count station, four 0.1256 ha (20 m radius) vegetation sampling plots were established, one centered on the point center and three others centered 60 m from the point center at compass bearings of 0°, 120°, and 240°. Within each plot, residual trees and snags were tallied by species and diameter class (3-10.9, 11-18.9, 19-26.9, 27-34.9, 35-42.9, ≥ 43 cm diameter at breast height, dbh). Each snag was also classified by height (1-2.9, 3-4.9, 5-9.9, ≥ 10 m) and decay class (7 classes, following the wildlife tree classification of BC, BC Environment 1995). The number of trees of each species that had established following the disturbance was counted within a 0.03 ha (10 m radius) nested subplot, by diameter class (1-2.9, 3-6.9, 7-110.9, 11-14.9, 15-18.9, 19-22.9, ≥ 23 cm dbh). The percent cover of shrubs was estimated within a 5 m radius (0.0079 ha) sub-plot, along with the percent cover and species of all shrubs with > 5 % cover. Percent cover of the five most abundant herbs was estimated within the same sub-plot. Coarse woody debris (CWD) was sampled along a 10 m transect oriented in a random direction from the center of the plot. All intersecting pieces of dead wood > 7 cm in diameter at the intersection point were tallied by diameter class and decay class, as per snags. Also within the 5 m radius subplot the total number of vertical vegetation layers was counted. In addition, I recorded the elevation and location of each point station center to 1-2 m with a differentially corrected GPS unit. Aspect was determined with a compass.

Data Analyses

Vegetation

The original vegetation data set contained over 100 variables. To reduce the data set for descriptive purposes, I chose a subset of 17 variables that summarized the main attributes of the vegetation likely to be important to birds (Table 2.1). Cavity snags were defined as western larch, Douglas-fir, and deciduous snags greater than 20 cm dbh, as these were the species and diameter classes most likely to have cavities (unpubl. data). I examined the distribution of each of these variables by disturbance type and subzone. I considered two point count stations to be outliers because of unusually high densities of understory conifer trees and removed these from analyses. I then generated means for each chosen variable from each of the four plots at each station, and used one-way ANOVA's to determine if the mean value of each variable differed between logged and burned stations. Variables that were not normally distributed were log-transformed, and I used a Kruskal-Wallis nonparametric ANOVA for variables that exhibited unequal variances between disturbance types. SAS version 6.12 (SAS, 1996) was used for all analysis.

Bird Community

Prior to analysis I removed data for all corvids, raptors, grouse, shorebirds, and kingfishers, as my point counts did not adequately sample these species. I also removed data for all woodpeckers except the Red-naped Sapsucker and Northern Flicker (scientific names in Appendix A). These latter two species are more conspicuous and thus more likely to be sampled by point counts than other species of woodpecker in the area. Data for birds detected flying over the canopy but not landing in the count area were deleted from the analysis. In addition, I considered all species detected fewer than 5 times each year or at less than 3 point count stations each year to be incidental and removed them from analysis.

Bird Detectability

The point count stations varied in vegetative structure and thus potentially in acoustical transmission. To examine potential biases in comparisons between burned and logged stands related to differences in detectability that could be associated with differences in vegetative structure, I examined the detection-by-distance frequency distributions for each species with > 50 detections. First, I deleted all observations of birds > 130 m from the point count center because distance estimates of taped vocalizations > 130 from the observer were imprecise. Then, for each species, using data pooled from three years and the detections of singing males only, I constructed frequency distributions of detections by distance class in 10 m intervals by disturbance type and age class. For each disturbance/age class combination, the distance within which 90 % of the detections were included was determined and the lowest

Table 2.1 Summary of site and vegetation variables from the point count stations. 'Burned' and 'Logged' values are untransformed means ± standard deviation, with minimum and maximum below in parentheses. Statistics in parentheses are a Chi-square from a Kruskal-Wallis non-parametric ANOVA. Residual deciduous trees in the ESSF were not tested because they were found at only two stations. Likewise, cavity snags in ESSF were found at only one logged station, thereby precluding a statistical test. † indicates the variable was log-transformed for one-way ANOVA analysis.

	ESSF				**MS**			
Variable	**Burned** (n=45)	**Logged** (n=27)	**F (χ^2)**	**p**	**Burned** (n=23)	**Logged** (n=79)	**F (χ^2)**	**p**
Sites								
Age † (yrs. since disturbance)	23.3 ± 10.6 (12-37)	18.9 ± 12.0 (5-37)	3.56	0.059	30.0 ± 13.9 (12-45)	21.7 ± 8.3 (5-41)	(3.64)	0.056
Elevation (m)	1721 ± 129 (1550-1950)	1653 ± 54 (1565-1793)	6.69	**0.02**	1466 ± 115 (1268-1640)	1329 ± 157 (1044-1631)	15.12	**<0.001**
Vegetation								
Residual Trees								
Conifer Overstory † (stems/ha >19cm dbh)	4.8 ± 6.9 (0-119)	4.9 ± 6.5 (0-119)	(0.21)	0.648	55.3 ± 62.7 (0-245)	55.9 ± 80.4 (0-320)	0.06	0.804
Basal Area Conifer † Overstory (m^2/ha)	1.16 ± 2.1 (0–8.9)	0.89 ± 1.6 (0-6.8)	0.24	0.627	4.7 ± 5.1 (0-18.4)	4.4 ± 6.1 (0-31.4)	0.21	0.650
Conifer Understory † (stems/ha < 19 cm dbh)	13.5 ± 34.6 (0-173)	75.7 ± 119 (0-471)	(11.69)	**0.006**	28.3 ± 45.9 (0-143)	52.5 ± 109 (0-831)	3.31	0.079
Deciduous † (stems/ha)	0	0.44 ± 0.82 (0-8)	not tested		2.4 ± 6.6 (0-24)	6.9 ± 14.2 (0-68)	2.75	0.100
Basal Area Deciduous † (m^2/ha)	0	0	not tested		0.03 ± 0.95 (0- 0.43)	0.24 ± 0.52 (0-2.93)	3.83	**0.050**

Continues:

Table 2.1 continued…

Variable	ESSF				MS			
	Burned (n=45)	**Logged** (n=27)	F (χ^2)	p	**Burned** (n=23)	**Logged** (n=79)	F (χ^2)	p
Snags and CWD								
Total number † (no./ha)	454.5 ± 501.4 (0-1766)	21.6 ± 28.1 (0-109)	26.92	**< 0.001**	204.3 ± 281.8 (0-1010)	20.7 ± 26.4 (0-177)	22.80	**< 0.001**
Cavity snags † (no./ha)	15.8 ± 16.2 (0-242)	0.01 ± 0.30 (0-2.0)	Not tested		30.4 ± 42.5 (0-163)	3.85 ± 4.80 (0-18)	52.15	< 0.001
Small CWD † (pieces < 27 cm diam./10 m)	23.5 ± 10.7 (6-62)	18.9 ± 7.7 (6-38)	3.94	**0.050**	33.0 ± 23.2 (9-102)	19.8 ± 10.4 (2-68)	9.81	**0.002**
Large CWD † (pieces > 27 cm diam./10 m)	2.09 ± 2.71 (0-12)	1.74 ± 2.71 (0-10)	(0.45)	0.499	1.43 ± 1.53 (0-4)	1.89 ± 2.80 (0-20)	0.03	0.870
Regeneration								
Conifers † (no./ha, non- pine)	1601 ± 2277 (0-10295)	2163 ± 1087 (0-4840)	(9.18)	**0.002**	2823 ± 2533 (287-10445)	1372 ± 1107 (48-5405)	9.17	**0.003**
Pine (no./ha)	2527 ± 1961 (0-8599)	477 ± 624 (0-2125)	(22.76)	**< 0.001**	1271 ± 1492 (0-5804)	496 ± 531 (0-2309)	(3.78)	**0.050**
Deciduous † (no./ha)	44.9 ± 106 (0-510)	37.1 ±61.8 (0-270)	0.11	0.740	381 ± 609 (0-2548)	507 ± 829 (0-3144)	0.01	0.940
Herbaceous Vegetation								
Shrub Cover (% cover)	34.2 ±20.1 (0-87)	51.3 ± 22.9 (0-88)	11.4	**< 0.001**	37.7 ± 20.0 (4–80)	48.6 ± 19.0 (14-98)	5.72	**0.018**
Shrub Richness (# spp.)	2.93 ± 1.28 (0-6)	3.81 ± 1.35 (1-7)	7.70	**0.007**	3.21 ± 1.26 (1-7)	3.84 ± 1.30 (1-8)	4.24	**0.042**
Herb Cover (% cover)	69.9 ± 42.7 (14-100)	68.5 ± 29.8 (25-100)	0.02	0.887	39.1 ± 22.7 (12-100)	36.2 ± 18.8 (8-100)	0.40	0.529
Grass (% cover)	18.2 ± 19.3 (0-65)	14.3 ± 19.2 (0-85)	0.70	0.405	20.9 ± 20.2 (0-65)	32.7 ± 20.7 (0-83)	0.51	**0.017**
No. of vertical layers	2.03 ± 0.83 (1– 4)	2.48 ± 0.78 (1–4)	5.24	**0.025**	2.42 ± 0.63 (1-4)	2.75 ± 0.71 (1-5)	3.8	**0.054**

distance of the six disturbance/age classes selected as the effective detection distance for that species (Hagar et al. 1996). All observations greater than this distance were deleted from further analysis. This approach should minimize differences in acoustical transmission among stand types. For species with < 50 detections there were not enough detections to examine differences among stand types and an effective radius of 100 m was used, which was the average detection radius of all species for which it was calculated.

Structure of the bird community

The diversity of the songbird community in each disturbance type in each subzone was compared using Simpson's diversity indices (Krebs 1989). The estimate of Simpson diversity is unbiased, making it valid to compare Simpson diversity in communities with different sample sizes (Lande et al. 2000). Diversity consists of two concepts, the number of species and their relative abundances (Krebs 1989). However, the latter concept, evenness, is often ignored (Magurran 1988). To graphically compare the evenness in each disturbance type, I used dominance-diversity (relative abundance) curves. These curves are plots of the rank of each species in the community (as assessed by mean abundance) against its abundance. Communities with a high degree of dominance and low diversity tend to have very steep curves on such a graph; those with low dominance and high diversity assume a more horizontal aspect (Brower et al. 1990). Curves were compared with Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1981:443).

Analyses of community structure and bird species diversity cannot be reliably done with simple count data because of differences in detectability among species (Carey et al. 1994). To account for differences in detectability, I calculated an index of density based on the number of birds detected within the effective detection radius for that species, divided by the area of a circle described by this radius.

Hypothesis tests for richness and abundance

I used stepwise multiple linear regression to test the hypothesis that disturbance type and intensity influence mean richness and abundance of songbirds, with bird assemblage and species abundance indices as response variables, disturbance type and three residual tree variables as explanatory variables, and elevation and stand age (years since disturbance) as covariates. The residual tree variables included numbers of conifer overstory trees (conifers with dbh $\geq$ 19 cm), conifer understory trees (conifers with dbh < 19 cm), and deciduous trees (all dbh classes included). An index of abundance was calculated as the mean number of individuals detected per station per visit per year. Species richness at a station was defined as the total number of species detected over the three visits each year, averaged over the three years of the study. I conducted the tests separately by biogeoclimatic subzone because preliminary analysis showed that the influence of elevation masked effects of other variables when subzones were not considered separately, and because of ecological differences between subzones. Tests were only done for species that occurred in > 2/3 of the point count stations in each subzone (Hosmer and Lemeshow 1989).

None of the potential explanatory variables were highly inter-correlated (highest r = 0.55 between deciduous trees and elevation and between conifer overstory and conifer understory trees, most r values were < 0.2). Regardless, with stepwise variable selection highly correlated variables will not be included in the same model (M. Huso, Dept. Forest Science, Oregon State University, pers. comm.). The deciduous tree variable was not used in the ESSF analysis as there were very few deciduous trees in this subzone. Prior to analysis, pairwise plots were examined for outliers and correlations. Vegetation variables were log-transformed to better meet the assumptions of normality. Response variables were tested for the assumptions of normality and constant variance and an over-dispersed Poisson regression used rather than MLR if the assumptions were not met. In all stepwise procedures, I set the P value at 0.25 for a variable to enter a model and at 0.10 for a variable to stay in a model. I selected these P values because of the relative ramifications of making Type II errors in applied research (Steidl et al. 1997).

Similarity Through Time

To determine if bird communities in logged and burned sites became more or less similar as the time since disturbance increased, I used two indices: Morisita's index of similarity and percentage similarity. Morisita's index reflects the probability that two individuals drawn randomly from each of two communities will belong to the same species

(Brower et al. 1990). Morisita's index varies from 0 (no similarity) to 1 (complete similarity), is nearly independent of sample size (Krebs 1989), and was recommended by Wolda (1981) as the best overall measure of similarity of ecological use. Percentage similarity is also little affected by sample size and by species diversity, and ranges from 0 (no similarity) to 100 (complete similarity, Krebs 1989). I calculated similarity between burned and logged stands among three age groups (9 – 19 yr., 20-29 yr., and > 30 yr. since disturbance). To better understand patterns underlying changes in similarity, I also calculated mean songbird richness and abundance per point count station for each of the disturbance/age classes noted above and compared values for each age class with an ANOVA and orthogonal contrasts. I examined changes through time for six vegetation variables (density of overstory conifers, density of understory conifers, density of snags, shrub cover, density of regenerating conifer trees, and density of regenerating pine trees) in a similar fashion. Finally, I compared the relative abundance of the 10 most dominant species (those with the highest relative abundance) in each disturbance/age class.

Results

Vegetation Patterns

Mean age of burned and logged stands was similar in both biogeoclimatic subzones, although there was a trend for logged stands to be a few years younger (Table 2.1). Mean elevation of burned stands was 68 m higher than that of logged stands in the ESSF and 137 m higher in the MS (Table 2.1). Burned and logged stands had similar densities and basal areas of residual conifer overstory trees. However, the density of understory conifers was higher in logged stands than in burned stands in the ESSF and there was a similar but non- significant trend in the MS (Table 2.1). In both subzones residual conifer overstory trees were almost entirely western larch (89.5% of all overstory residuals), followed by spruce (6.4%), and Douglas-fir (2.2%). Rarely were lodgepole pine (1.6%) and never were subalpine fir (0%) found as residual trees. Logged stands in the MS had a greater basal area of residual deciduous trees and a trend towards a higher density of these. In both subzones burned stands had a greater density of snags, including cavity snags, as well as pieces of small CWD. The amount of large CWD did not differ statistically between the two disturbance types. Burned stands had higher densities of regenerating pine trees in both subzones, but the density of conifers other than lodgepole pine was higher in logged stands in the ESSF and higher in burned stands in the MS. The density of regenerating deciduous trees was similar for both disturbance types in both subzones. In both subzones shrub cover and shrub richness was higher in logged stands whereas herb cover did not differ, but logged stands in the MS had a higher percent cover of grass. Shrub species with the greatest mean percent cover differed slightly between burned and logged stands in both subzones, mainly in the ESSF. In the ESSF, burned stands were dominated by false azalea (11.7%), buffaloberry (8.0%), willow (6.0%), and Sitka alder (4.0%); logged stands by Sitka alder (15.8%), false azalea (9.8%), Utah honeysuckle (4.4%), and thimbleberry (4.4%). In the MS, burned stands were dominated by alder (7.9%), willow (5.9%), buffaloberry (5.0%), and rose (3.6%); logged stands by buffaloberry (7.8%), alder (7.1%), rose (4.9%), and saskatoon (4.6%). Logged stands had a higher mean number of vertical vegetation layers in both subzones.

Structure of the Bird Community

Over the three years of the study, 20,319 detections of 87 species of birds were made. After omitting non-songbird species, there were 19,063 detections of 63 species. Non-songbird species detected but not analyzed included Belted Kingfisher, Canada Goose, six corvids (Blue Jay, Steller's Jay, Gray Jay, Clark's Nutcracker, American Crow, and Common Raven), five woodpeckers (Downy Woodpecker, Hairy Woodpecker, Three-toed Woodpecker, Black-backed Woodpecker, and Pileated Woodpecker), two shorebirds (Killdeer and Solitary Sandpiper), three grouse (Ruffed Grouse, Spruce Grouse, and Blue Grouse), three raptors (Northern Goshawk, Red-tailed Hawk, and American Kestrel) and three owls (Great-horned Owl, Northern Pygmy Owl, and Boreal Owl). Excluding incidental detections left 19,002 detections of 45 songbird species for analysis.

Songbird communities in both biogeoclimatic subzones were dominated by Dark-eyed Junco, Yellow-rumped Warbler, and Wilson's Warbler (Table 2.2). In the MS, most frequently detected species also included the Dusky Flycatcher, Warbling Vireo, Orange-crowned Warbler, Townsend's Warbler, Pine Siskin and Swainson's Thrush. Thirteen species made up 75 % of the total number of detections for both burned and logged stands in the MS, and nine of the ten most abundant species in each disturbance type were the same (Table 2.2).

Table 2.2 The 10 most abundant species in each disturbance type, in terms of the percentage of the total community they comprise, by biogeoclimatic subzone. Within each subzone, species present in one disturbance type and not the other are shown in italics.

	Burned		**Logged**	
	Species	**%**	**Species**	**%**
MS	Yellow-rumped Warbler	13.9	Dark-eyed Junco	14.7
	Dark-eyed Junco	10.7	Yellow-rumped Warbler	8.9
	Wilson's Warbler	8.6	Dusky Flycatcher	7.6
	Dusky Flycatcher	6.8	Orange-crowned Warbler	6.0
	Warbling Vireo	6.5	*Chipping Sparrow*	5.4
	Townsend's Warbler	4.6	Wilson's Warbler	5.3
	Pine Siskin	4.5	Warbling Vireo	4.8
	Swainson's Thrush	4.5	Swainson's Thrush	4.6
	Orange-crowned Warbler	3.8	Townsend's Warbler	4.6
	Cassin's Vireo	3.6	Pine Siskin	4.3
ESSF	Dark-eyed Junco	18.9	Dark-eyed Junco	18.0
	Yellow-rumped Warbler	14.1	Wilson's Warbler	14.1
	Wilson's Warbler	8.9	Yellow-rumped Warbler	7.7
	Hermit Thrush	5.7	Warbling Vireo	6.9
	Dusky Flycatcher	5.5	Chipping Sparrow	5.1
	Pine Siskin	3.9	*Townsend's Warbler*	4.7
	Warbling Vireo	3.7	*MacGillivray's Warbler*	4.4
	Townsend's Solitaire	3.7	Hermit Thrush	3.7
	Swainson's Thrush	3.5	*Fox Sparrow*	3.6
	Chipping Sparrow	3.2	Swainson's Thrush	3.2

In the ESSF most frequently detected species also included Hermit Thrush, Warbling Vireo, and Chipping Sparrow, and twelve species comprised 75 % of the detections in both disturbance types. Seven of the ten most abundant species were the same for both disturbance types (Table 2.2).

Simpson's diversity indices were nearly identical for logged (0.940) and burned (0.937) sites in the MS, and for logged (0.920) and burned (0.917) stands in the ESSF. The evenness of the bird community was also very similar in burned and logged stands in both the MS and the ESSF , as indicated by the similar shapes of the dominance-diversity curves (Figure 2.2, Kolmogorov-Smirnov 2 sample tests, ESSF, $D = 0.0197$, $n_1=n_2=30$, $p > 0.10$; MS, $D = 0.0349$, $n_1=n_2=30$, $p > 0.10$). In both disturbance types and subzones the curves were strongly curved, indicating dominance by a few species. These curves also reflect the higher abundance of birds in logged stands, particularly in the ESSF, as the curve for logged stands is above that for burned stands.

Richness and Abundance Hypothesis Tests

Mean species richness per station and mean abundance per station were higher for logged stands than for burned stands (Table 2.3, Table 2.4). In the MS, richness was negatively associated with elevation and positively with residual broadleaf trees and logging, while abundance was negatively associated with elevation and stand age, and positively with residual broadleaf trees and logging (Table 2.3). In the ESSF both richness and abundance were negatively associated with elevation and positively with residual conifer understory trees and logging (Table 2.4, note that broadleaf trees were not included in the ESSF analysis as there were few of them in this subzone).

Of the 23 species individually examined in the MS, eight had statistically higher mean abundances in logged stands (Chipping Sparrow, Dark-eyed Junco, Golden-crowned Kinglet, Mountain Chickadee, Orange-crowned Warbler, Ruby-crowned Kinglet, Swainson's Thrush, Townsend's Warbler), five were statistically higher in burned stands (Cassin's Vireo, Red-breasted Nuthatch, Townsend's Solitaire, Western Tanager, Yellow-rumped Warbler), and there was no statistically significant difference for the remaining ten (Table 2.3). Species showing particularly strong responses to logging included Townsend's Warbler (4.44 times higher in logged stands, after accounting for other terms in the model) and Swainson's Thrush

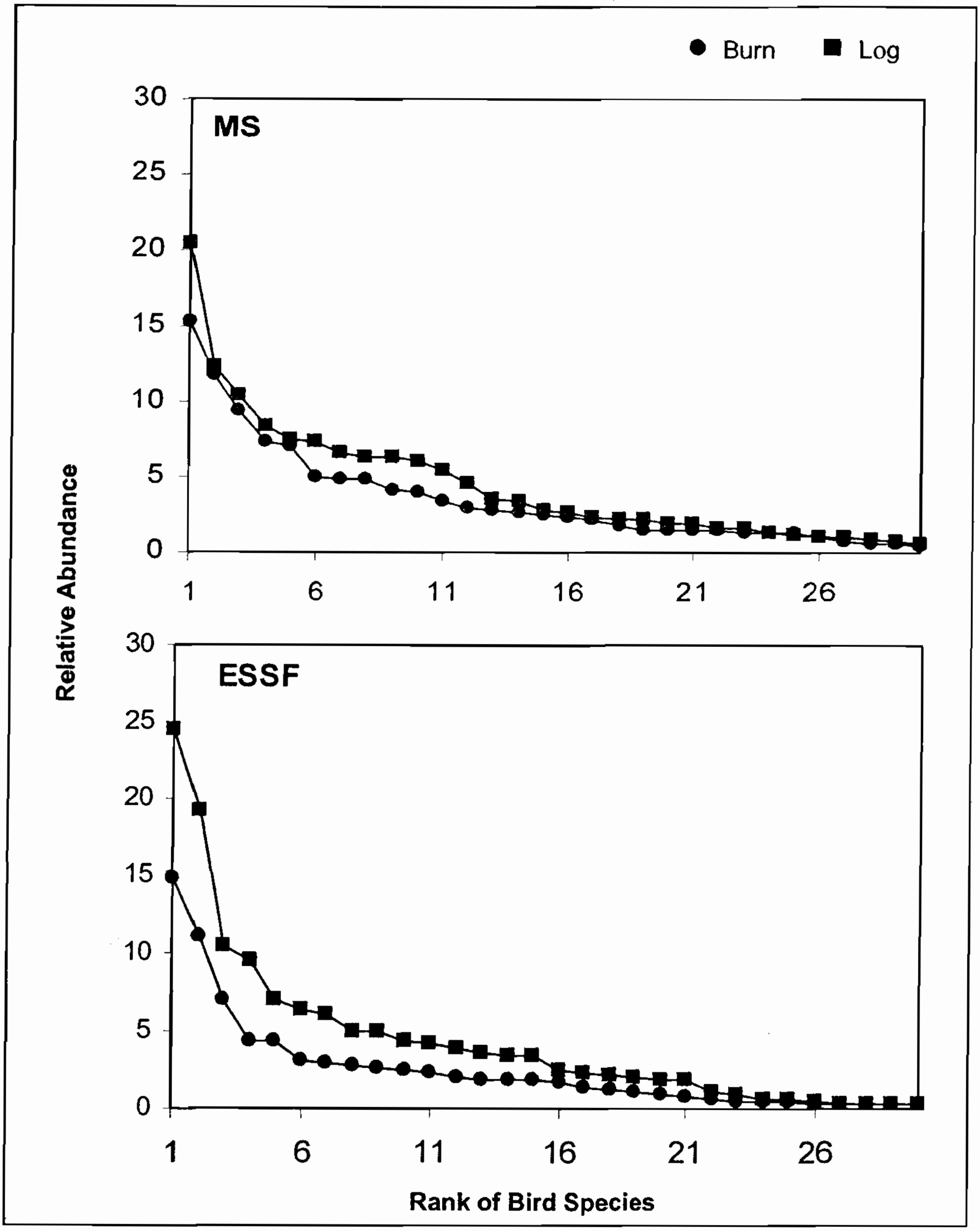


Figure 2.2: Dominance-diversity curves for each disturbance type, by biogeoclimatic zone for the top 30 species in each community by mean abundance. No difference between the curves in either disturbance type, Kolmogorov-Smirnov 2-sample tests, p's > 0.10.

(2.06 times higher) in the MS (Table 2.3) and Fox Sparrow (3.12 times higher) and Ruby-crowned Kinglet (2.89 times higher) in the ESSF (Table 2.4) . Estimates of mean abundance are shown in Table 2.5. Of the residual tree variables, conifer overstory trees entered into more individual species models (16) than did conifer understory trees (9 models) or broadleaf trees (8 models). Associations with residual conifer overstory trees were positive for some species, including those known to nest or forage in mature conifer trees such as Townsend's Warbler and Golden-crowned Kinglet, and negative for others, reflecting the preference for open and early seral stands of species such as Dark-eyed Junco, Orange-crowned Warbler, and American Robin. Most species that increased in relation to the density of conifer overstory trees did so fairly strongly. For example, the Golden-crowned Kinglet had a partial regression coefficient of 1.36, indicating that, for stands of similar age and disturbance type, doubling the number of conifer overstory trees produced an increase of 36 % in median abundance. Associations of abundance with residual conifer understory trees were negative for 7 of 9 models, but the partial regression coefficients were generally smaller than those for overstory trees. Only Dark-eyed Junco and Olive-sided Flycatcher were positively associated with understory trees in the MS. Associations with broadleaf trees were positive for all species, except for the Yellow-rumped Warbler. The magnitude of the partial regression coefficients for broadleaf trees were similar to those for conifer overstory trees, indicating a strong association between abundance and broadleaf trees.

Elevation was a significant covariate in 15 of the 24 species models for the MS, with a negative effect for all but three species (Townsend's Warbler, Wilson's Warbler, Hermit Thrush). Partial regression co-efficients for most species ranged from 0.997 – 0.999, implying a decrease in median abundance of 10-30 % for every 100 m increase in elevation after accounting for the other terms in the models. Four species, the Cassin's Vireo, Western Tanager, Black-capped Chickadee, and Red-naped Sapsucker had partial coefficients of 0.993 – 0.995, indicating decreases in median abundance of 50 – 70 % for every 100 increase in elevation given the other terms in each model. These were all species whose abundance was extremely low in the ESSF, and two of them (Red-naped Sapsucker and Black-capped Chickadee) were strongly influenced by the density of broadleaf trees, which declined in abundance with elevation. In the ESSF, elevation entered into 10 of the 20 species models, with a negative effect in each case.

In the ESSF, associations with logging were more pronounced than in the MS. Of the 20 species examined, 11 were more abundant in logged stands (Hermit Thrush, Dark-eyed

Table 2-3. Results of the statistical hypothesis tests for the MS. Values in the table are partial regression coefficients with 95 % confidence intervals in parentheses (back-transformed parameter estimates). Interpretations are in terms of median abundance, and are dependent on all terms in the model. Logged stands were used as a reference level, so the value in the **Disturbance** column indicates how many times greater the median abundance in logged stands was relative to burned stands. **Residual tree type** variables were log-transformed for the regression, so effect sizes are interpreted in terms of a doubling of residual tree density. Absence of values indicates variables which did not enter or stay in the model. For example, for the Orange-crowned Warbler, the interpretation of coefficients is as follows: for stands of similar disturbance type and conifer overstory an increase in elevation of 100 m led to a decrease of 20 % in median abundance (0.002 decrease per m); for stands of similar elevation and residual conifer overstory density, the median abundance was 1.42 times higher in logged stands than burned stands; and for stands of similar disturbance type and elevation doubling the density of conifer overstory trees led to a median abundance of 0.92 times, or a decrease of 8 %. The number of stars beside the estimate indicates the magnitude of the p value: * < .10, **< .01, *** < .001. † indicates a quasi-likelihood regression was used (r^2_{adj} not applicable), otherwise multiple linear regression was used. p values for all models <0.0001.

		Co-variates			***Residual Tree Types***			
	Dependent Variable	**Elevation**	**Age**	**Disturbance**	**Conifer Overstory**	**Conifer Understory**	**Broadleaf**	**r^2_{adj} model**
Higher in Logged	Richness	0.995 *** (0.992 – 0.998)		2.93 * (0.93 – 8.66)			2.27 *** (1.63 – 3.18)	0.42
	Total Abundance	0.995 *** (0.993 – 0.997)	0.95 ** (0.91 – 0.99)	2.49 * (0.90 – 6.86)			1.48 ** (1.11 – 1.98)	0.34
	Chipping Sparrow	0.999 *** (0.998 – 0.999)		1.29 * (0.98 – 1.71)	0.89 *** (0.85 – 0.93)			0.45
	Dark-eyed Junco		0.98 *** (0.97-0.99)	1.36 *** (1.14 – 1.62)	0.93 *** (0.90 – 0.96)	1.04 ** (1.00 – 1.08)		0.46
	Golden-crowned Kinglet †		1.06 *** (1.04 – 1.09)	1.64 * (0.91 – 2.93)	1.36 *** (1.19 – 1.54)			
	Mountain Chickadee			1.47 *** (1.11 – 1.94)	1.20 *** (1.13 – 1.26)	0.91 *** (0.86 – 0.96)	1.12 *** (1.04 – 1.21)	0.40
	Orange-crowned Warbler	0.998 *** (0.997 - 0.999)		1.42 ** (0.99 - 2.02)	0.92 ** (0.86 – 0.98)			0.23

continues…

Table 2.3 continued…

		Co-variates			*Residual Tree Types*			
	Dependent Variable	**Elevation**	**Age**	**Disturbance**	**Conifer Overstory**	**Conifer Understory**	**Broadleaf**	**r^2_{adj} model**
Higher in Logged (cont'd)	Ruby-crowned Kinglet†		1.02 * (1.00 – 1.04)	1.86 ** (1.09 – 3.15)	1.18 *** (1.08 – 1.28)		1.28 *** (1.16 – 1.41)	
	Swainson's Thrush		1.03 *** (1.02 – 1.05)	2.06 *** (1.57 – 2.71)	1.16 *** (1.10 – 1.23)	0.87 *** (0.82 – 0.92)		0.52
	Townsend's Warbler †	1.002 ** (1.00 – 1.003)	1.08 *** (1.06 – 1.11)	4.44 *** (2.52 - 7.81)	1.27 *** (1.15 – 1.41)			
Higher in Burned	Cassin's Vireo†	0.993 *** (0.991 – 0.995)		0.18 *** (0.09 – 0.34)	1.21 * (1.05 – 1.40)	0.90 * (0.80 – 1.01)		
	Red-breasted Nuthatch †	0.998 * (0.996 – 1.000)		0.41 *** (0.22 – 0.75)	1.41 *** (1.24 – 1.60)		1.28 ** (1.11 – 1.48)	
	Townsend's Solitaire†			0.63 * (0.41 – 0.98)	0.89 ** (0.81 – 0.97)			
	Western Tanager	0.993 *** (0.001 – 0.995)	0.98 * (0.96 – 1.00)	0.46 * (0.23 – 0.92)	1.23 *** (1.09 – 1.39)	0.90 * (0.82 – 0.99)		
	Yellow-rumped Warbler	0.999 *** (.998 – 1.000)	0.986 *** (0.98 – 0.99)	0.60 *** (0.49 - 0.74)			0.95 * (.90 – 1.00)	0.21
No detectable Difference	Wilson's Warbler	1.002 *** (1.001 – 1.003)	0.98 ** (0.97 – 0.99)					0.20
	Black-capped Chickadee †	0.994 *** (0.992 – 0.996)	1.04 *** (1.02 – 1.07)			0.86 *** (0.79 – 0.94)	1.25 *** (1.01 – 1.25)	

continues…

Table 2.3 continued..

		Co-variates			*Residual Tree Types*			
	Dependent Variable	**Elevation**	**Age**	**Disturbance**	**Conifer Overstory**	**Conifer Understory**	**Broadleaf**	**r^2_{adj} model**
no detectable difference (cont'd)	Dusky Flycatcher †	0.999 * (0.998 – 1.000)	0.94 *** (0.93 – 0.96)		0.88 *** (0.82 – 0.94)		1.15 ** (1.04 – 1.28)	
	Hermit Thrush †	1.001 * (1.000 – 1.003)				0.89 * (0.82 – 0.98)		
	Warbling Vireo					0.94 * (0.88 – 1.01)	1.16 ** (1.04 – 1.29)	0.08
	Red-naped Sapsucker †	0.995 *** (0.993 – 0.997)			1.10 * (1.00 – 1.22)		1.20 ** (1.05 – 1.36)	
	Northern Flicker †	0.997 *** (0.996 – 0.998)	0.97 * (0.95 – 0.99)					
	American Robin	0.998 *** (0.997 – 0.999)	0.99 ** (0.98 – 1.00)		0.96 * (0.91 – 1.00)			0.32
	Olive-sided Flycatcher †		0.95 *** (0.93 – 0.97)			1.07 * (1.00 – 1.18)		
	Pine Siskin		0.98 ** (0.97 – 0.99)			1.09 ** (1.03 – 1.15)		0.15
	MacGillivray's Warbler †	0.997 *** (0.996 – 0.998)	0.98 ** (0.96 – 0.99)		0.91 ** (0.86 – 0.97)			

Table 2.4 Results of the hypothesis tests for the ESSF. See Table 3 for an explanation of table values. Note: there were very few broadleaf trees in the ESSF, so this variable was not permitted to enter the models.

		Co-variates			**Residual Tree Types**		
	Dependent Variable	**Elevation**	**Age**	**Disturbance**	**Conifer Overstory**	**Conifer Understory**	r^2_{adj}
Higher in Logged	Richness	0.988 *** (0.982 – 0.984)		16.3 *** (3.71 – 72.5)		1.32 * (1.00 – 1.74)	0.45
	Total Abundance	0.992 *** (0.988 – 0.996)		30.98 *** (9.77 – 97.48)		1.30 * (1.05 – 1.61)	0.61
	Hermit Thrush		1.04 *** (1.03 – 1.05)	1.42 ** (1.10 – 1.83)			0.39
	Dark-eyed Junco		0.98 *** (0.98-0.99)	1.36 *** (1.18 – 1.56)			0.36
	Warbling Vireo	0.997 *** (0.995 – 0.998)	1.03 *** (1.01 – 1.04)	2.30 *** (1.71 – 3.08)			0.57
	Wilson's Warbler	0.997 *** (0.995 – 0.998)	1.03 *** (1.01 – 1.04)	2.16 *** (1.51 – 3.09)		1.07 * (1.00 – 1.15)	0.51
	Fox Sparrow †		1.03 * (1.00 – 1.06)	3.12 *** (1.78 – 5.52)			
	Swainson's Thrush		1.04 *** (1.03 – 1.05)	1.40 * (1.05 – 1.89)		1.09 ** (1.03 - 1.17)	0.42
	Chipping Sparrow †	0.994 *** (0.991 – 0.997)		1.67* (1.05 – 2.64)		1.09 * (1.00 – 1.18)	
	MacGillivray's Warbler †	0.994 *** (0.990 – 0.997)		2.68 *** (1.67 – 4.32)			
	Olive-sided Flycatcher †		0.97 *** (0.95 – 0.99)	1.75 ** (1.06 – 2.90)		1.15 *** (1.05 – 1.25)	

continues…

Table 2.4 continued…

		Co-variates			Residual Tree Types		
	Dependent Variable	**Elevation**	**Age**	**Disturbance**	**Conifer Overstory**	**Conifer Understory**	r^2_{adj}
Higher in Logged (cont'd)	Townsend's Warbler †	0.994 *** (.0991 – 0.998)		2.80 *** (1.62 – 4.87)	1.18 * (1.03 – 1.34)	1.09 * (0.98 – 1.21)	
	Ruby-crowned Kinglet†		1.04 *** (1.02 – 1.06)	2.89 *** (1.68 – 4.98)			
Higher in Burned	Yellow-rumped Warbler	0.999 * (.997 – 1.000)		0.83 * (0.68 – 1.02)			0.08
	Townsend's Solitaire		0.97 *** (0.96 – 0.98)	0.76 * (0.59 – 0.97)			0.29
	Northern Flicker †	0.992 *** (0.987 – 0.997)	0.97 * (0.94 – 1.00)	0.40 ** (0.62 – 0.80)			
No detectable Difference	Orange-crowned Warbler	0.997 *** (0.997 - 0.998)	1.02 * (0.98 – 1.05)				0.27
	Mountain Chickadee †				1.19 *** (1.05 – 1.36)		
	Dusky Flycatcher †	0.997 * (0.993 – 1.000)				0.87 (0.77 – 0.99)	
	White-crowned Sparrow †	0.995 (0.991 – 1.000)	0.96 (0.93 – 0.99)				
	Pine Siskin		0.98 ** (0.97 – 0.99)		1.11 ** (1.03 – 1.21)		0.21
	American Robin		0.97 *** (0.96 – 0.99)				0.22

Junco, Warbling Vireo, Wilson's Warbler, Fox Sparrow, Swainson's Thrush, Chipping Sparrow, MacGillivray's Warbler, Olive-sided Flycatcher, Townsend's Warbler, Ruby-crowned Kinglet), three were higher in burned stands (Yellow-rumped Warbler, Townsend's Solitaire, Northern Flicker), and there was no statistically significant difference for the remaining six (Orange-crowned Warbler, Mountain Chickadee, Dusky Flycatcher, White-crowned Sparrow, Pine Siskin, American Robin, Table 2.4). Residual conifer overstory trees entered in only three models (Mountain Chickadee, Pine Siskin, Townsend's Warbler), likely due to the lower densities of these trees in the ESSF as compared to the MS. However, each of these species was positively associated with residual conifer overstory trees. Conifer understory trees entered into six models with positive coefficients for all but one species (Dusky Flycatcher). After accounting for other terms in the models, doubling the density of conifer understory trees was associated with an increase in median abundance of 7–15 % for these species.

Species associations with disturbance type were relatively consistent between the two subzones. No species was positively associated with logging or burning in one subzone and negatively associated in the other. However, models for a few species included disturbance as a significant influence in one subzone, but not in the other (e.g., Orange-crowned Warbler and Mountain Chickadee). For many species the association with residual trees differed between subzones, with different residual tree variables entering into the models in each subzone. This likely reflects the differing abundance of the residual tree types in the subzones (Table 2.1), rather than a change in habitat preference by these species.

Abundance and Frequency of Occurrence for Individual Species

Considering both the MS and the ESSF, there were no species detected in burned stands that were not also detected in logged stands, and only two species detected in logged stands and not in burned stands (Table 2.5). These two species, Western Wood Pewee and Brown-headed Cowbird, were detected at very few point count stations (4–7 %) and at very low abundance (Table 2.5). In the MS most species (36 of 45) were found at an equal or higher percentage of logged stations than burned stands. Only the Varied Thrush was found at greater than 20 % more burned stands than logged stands. However, the pattern for this species was reversed in the ESSF, where it occurred at a higher percentage of logged stations.

Table 2.5 The effective detection distance (m), mean abundance of birds per 40 ha (*Density and SE*), and percentage (%) of point count stations in each disturbance type at which each species was detected for all species detected at least 5 times each year or in at least 3 point count stations per subzone. Zero's are indicated with dashes. Values must be interpreted cautiously because they are not adjusted for elevation. Thus, simple comparisons of abundance may not match results from the regression hypothesis tests where elevation was allowed to enter as a covariate (e.g. Western Tanager).

	Effective detection	MS						ESSF					
		Burned			Logged			Burned			Logged		
Species	**distance**	**Density**	**SE**	**%**	**Density**	**SE**	**%**	**Density**	**SE**	**%**	**Density**	**SE**	**%**
American Robin	120	2.03	0.35	74	3.01	0.27	85	1.59	0.27	67	3.01	0.44	85
Black-capped Chickadee	100	1.53	0.38	48	1.91	0.25	53	0.38	0.13	18	0.38	0.13	26
Brewer's Sparrow	100	0.11	0.11	4	0.06	0.03	5	0.22	0.13	9	0.19	0.09	15
Brown Creeper	100	0.05	0.05	4	0.14	0.06	8	0.02	0.02	2	0.11	0.07	7
Brown-headed Cowbird	100	-	-	-	0.08	0.04	6	-	-	-	0.04	0.04	4
Cassin's Finch	100	0.11	0.07	9	0.14	0.04	11	0.27	0.12	13	0.06	0.06	4
Cassin's Vireo	100	3.95	1.02	61	1.91	0.38	48	-	-	-	0.25	0.13	15
Cedar Waxwing	100	0.15	0.12	9	0.16	0.06	9	0.06	0.04	4	0.21	0.14	7
Chipping Sparrow	100	3.44	0.51	96	7.52	0.51	95	2.55	0.51	58	7.01	0.89	85
Dark-eyed Junco	100	4.08	1.02	100	8.28	0.64	100	1.91	0.38	100	3.57	0.76	100
Dusky Flycatcher	90	7.71	2.04	61	10.54	0.94	83	4.88	1.10	51	4.25	0.94	74
Fox Sparrow	100	1.40	0.38	39	0.51	0.13	20	1.91	0.38	51	4.97	1.02	67
Golden-crowned Kinglet	80	2.59	0.80	48	2.59	0.40	46	0.20	0.14	9	0.80	0.40	30
Hammond's Flycatcher	70	2.63	0.75	43	2.21	0.57	37	0.49	0.18	16	0.70	0.31	18
Hermit Thrush	120	2.48	0.44	78	1.59	0.18	65	4.69	0.53	93	5.04	0.71	93
Lincoln's Sparrow	90	0.16	0.16	4	0.39	0.16	10	0.19	0.09	9	0.52	0.31	15
MacGillivray's Warbler	90	2.83	0.63	78	2.04	0.47	86	1.89	0.47	42	5.98	0.79	89

continues…

Table 2.5 continued…

	Effective	MS						ESSF					
	detection	Burned			Logged			Burned			Logged		
Species	distance	Density	SE	%	Density	SE	%	Density	SE	%	Density	SE	%
Mountain Bluebird	90	0.16	0.11	9	0.20	0.08	8	0.41	0.14	18	0.16	0.11	7
Mountain Chickadee	100	2.93	0.51	78	4.59	0.51	81	2.42	0.38	60	2.17	0.51	63
Northern Flicker	120	0.71	0.18	39	1.06	0.18	54	0.97	0.18	47	0.71	0.27	41
Olive-sided Flycatcher	120	1.33	0.35	52	2.21	0.27	71	1.33	0.27	58	4.16	0.62	82
Orange-crowned Warbler	100	4.08	1.02	74	8.28	0.64	90	1.91	0.38	49	3.57	0.76	81
Pine Grosbeak	100	0.05	0.05	4	0.20	0.11	6	0.21	0.12	7	0.26	0.13	15
Pine Siskin	90	5.72	1.20	78	6.88	0.66	86	4.02	0.72	67	4.28	0.93	67
Purple Finch	100	0.15	0.15	4	0.07	0.04	5	0.02	0.02	2	0.20	0.12	11
Red-breasted Nuthatch	120	1.42	0.35	61	1.15	0.18	44	0.53	0.09	36	0.09	0.09	18
Red-eyed Vireo	100	0.11	0.11	9	0.37	0.09	21	-	-	-	-	-	-
Red-naped Sapsucker	100	0.51	0.13	30	2.68	0.38	57	0.38	0.13	22	0.38	0.13	22
Ruby-crowned Kinglet	120	1.50	0.27	65	3.36	0.35	77	0.88	0.18	40	1.86	0.35	78
Rufous Hummingbird	70	1.33	0.57	26	2.73	0.60	39	1.48	0.49	24	2.73	0.60	56
Swainson's Thrush	120	4.87	0.80	92	6.37	0.44	92	2.83	0.44	75	4.42	0.53	85
Townsend's Solitaire	110	2.21	0.42	78	1.58	0.21	66	2.95	0.32	82	2.42	0.53	78
Townsend's Warbler	100	5.10	1.66	61	6.37	0.89	68	2.17	0.51	40	6.50	0.76	89
Varied Thrush	130	0.54	0.14	48	0.83	0.23	27	0.46	0.14	27	1.98	0.47	70
Veery	100	-	-	-	0.01	0.01	1	0.05	0.03	4	0.04	0.04	4
Vesper Sparrow	100	0.05	0.05	4	0.04	0.04	1	0.22	0.12	9	0.24	0.15	11
Warbling Vireo	90	7.23	1.57	87	6.61	0.63	80	3.15	0.79	51	9.44	1.42	85
Western Flycatcher	100	-	-	-	0.24	0.07	14	0.05	0.03	4	-	-	-
Western Tanager	110	1.68	0.53	56	2.84	0.42	56	0.11	0.11	4	0.32	0.11	11

continues…

Table 2.5 continued…

		MS						ESSF					
		Burned			Logged			Burned			Logged		
Species	**Effective detection distance**	**Density**	**SE**	**%**	**Density**	**SE**	**%**	**Density**	**SE**	**%**	**Density**	**SE**	**%**
Western Wood-Peewee	100	-	-	-	0.07	0.04	5	-	-	-	0.11	0.07	7
White-crowned Sparrow	120	0.35	0.18	22	0.62	0.18	23	1.24	0.35	38	1.95	0.53	63
White-winged Crossbill	100	0.15	0.12	9	0.28	0.07	18	0.02	0.02	2	0.13	0.07	11
Wilson's Warbler	90	9.44	2.04	87	7.39	0.79	92	7.39	1.10	82	19.34	1.73	100
Winter Wren	110	0.99	0.38	35	0.77	0.22	28	0.63	0.21	27	1.04	0.22	56
Yellow-rumped Warbler	100	15.29	1.40	100	12.36	0.64	100	11.46	0.89	100	10.57	0.76	100

This may reflect a preference for high elevations, rather than a difference between disturbance types. In the ESSF, 41 of 45 species occurred at an equal or higher percentage of logged stations than burned ones. However, none of the four species that occurred in a higher percentage of burned stations, Cassin's Finch, Mountain Bluebird, Northern Flicker, and Red-breasted Nuthatch, showed differences greater than 20 %. Dark-eyed Junco and Yellow-rumped Warbler were detected at every station in both subzones (Table 2.5).

Similarity Through Time

In the ESSF, both Morisita's index and percentage similarity increased with stand age (Table 2.6), indicating a convergence in songbird community structure through time. Similarly, richness and abundance converged with increasing time since disturbance (Figure 2.3). The number of similar species dominating each community also increased with time (Table 2.7). In all age/disturbance classes the community was dominated mainly by ground- and shrub-nesting birds.

Table 2.6 Similarity indices for songbird communities in logged and burned stands of three age classes.

Yrs. since disturbance	MS		ESSF	
	Morisita's Index	Percent Similarity	Morisita's Index	Percent Similarity
9 – 19	0.94	81.2	0.78	71.7
20 – 29	0.77	68.1	0.91	74.6
30 - 41	0.81	68.5	0.96	83.6

In the MS, however, patterns are less clear. Both Morisita's index and percentage similarity decreased from 9-19 yrs. to 20-29 yrs., but showed little change from 20-29 yr. to > 30 yrs. (Table 2.6). Richness and abundance tended to become slightly more similar through time (Figure 2.3), but patterns were not as distinct as in the ESSF. The number of similar species in the ten most abundant species declined through time (Table 2.8). In both burned and logged communities in the MS there was a clear trend for early seral ground- and shrub-nesting species such as Dusky Flycatcher and Wilson's Warbler to become less prevalent through time, and tree-nesting species such as Townsend's Warbler and Golden-crowned Kinglet to become more relatively abundant (Table 2.8).

Trends in vegetation components through time in each subzone were similar to those observed in the bird communities. In the ESSF, residual conifer overstory, conifer understory, and snags became more similar through time, whereas regenerating trees showed little change (Figure 2.4). Shrubs, were still significantly different in the oldest age class, although the magnitude of the difference decreased. In the MS, however, only conifer understory and snags became more similar; shrub cover, regenerating trees, and residual overstory conifers became less similar or showed little change (Figure 2.5). Particularly noticeable was the difference in residual overstory conifer trees between burned and logged stands > 30 yr. (Figure 2.5).

Table 2.7 The 10 most abundant species in each disturbance type, by age class, in the ESSF.

	9 – 19 Yrs. Post Dist.	**%**	**20 – 29 Yrs. Post Dist.**	**%**	**30 – 41 Yrs. Post Dist.**	**%**
LOGGED	Dark-eyed Junco	17.0	Dark-eyed Junco	16.4	Wilson's Warbler	17.2
	Wilson's Warbler	15.8	Wilson's Warbler	13.0	Dark-eyed Junco	13.7
	Warbling Vireo	7.0	Warbling Vireo	9.2	Yellow-rumped Warbler	9.8
	Yellow-rumped Warbler	6.8	Yellow-rumped Warbler	6.4	Hermit Thrush	8.4
	Chipping Sparrow	6.4	Orange-crowned Warbler	5.2	Warbling Vireo	7.6
	MacGillivray's Warbler	4.8	Chipping Sparrow	5.1	Fox Sparrow	5.9
	Townsend's Warbler	4.7	MacGillivray's Warbler	5.0	Townsend's Warbler	4.6
	Olive-sided Flycatcher	4.3	Townsend's Warbler	4.8	Swainson's Thrush	4.3
	Pine Siskin	3.7	Dusky Flycatcher	4.5	MacGillivray's Warbler	3.9
	Fox Sparrow	3.7	Fox Sparrow	3.8	Orange-crowned Warbler	2.7
	Similar Species = 6		***Similar Species = 6***		***Similar Species = 8***	
BURNED	Dark-eyed Junco	23.0	Dark-eyed Junco	17.3	Dark-eyed Junco	15.1
	Yellow-rumped Warbler	15.6	Yellow-rumped Warbler	13.4	Wilson's Warbler	13.1
	Dusky Flycatcher	8.8	Wilson's Warbler	10.6	Yellow-rumped Warbler	12.8
	Pine Siskin	6.5	Hermit Thrush	6.5	Hermit Thrush	8.4
	Townsend's Solitaire	5.6	Townsend's Warbler	6.1	Warbling Vireo	6.8
	Wilson's Warbler	4.4	Swainson's Thrush	5.0	Swainson's Thrush	5.1
	Chipping Sparrow	3.7	Warbling Vireo	3.8	Dusky Flycatcher	4.8
	American Robin	3.3	Rufous Hummingbird	3.6	MacGillivray's Warbler	3.6
	Olive-sided Flycatcher	2.9	Fox Sparrow	3.3	Mountain Chickadee	3.2
	Hermit Thrush	2.9	American Robin	2.9	Orange-crowned Warbler	3.0

Table 2.8 The 10 most abundant species in each disturbance type, by age class, in the MS.

	9 – 19 yrs. post-dist.	%	20 – 29 yrs. post-dist.	%	30 - 41 yrs. post-dist.	%
LOGGED	Dark-eyed Junco	15.7	Dark-eyed Junco	16.9	Townsend's Warbler	15.4
	Dusky Flycatcher	10.1	Yellow-rumped Warbler	9.7	Dark-eyed Junco	11.3
	Yellow-rumped Warbler	9.2	Dusky Flycatcher	7.6	Swainson's Thrush	7.3
	Orange-crowned Warbler	6.3	Warbling Vireo	6.4	Golden-crowned Kinglet	6.5
	Pine Siskin	6.1	Chipping Sparrow	6.1	Yellow-rumped Warbler	6.2
	Chipping Sparrow	5.9	Orange-crowned Warbler	6.1	Orange-crowned Warbler	5.4
	Wilson's Warbler	5.6	Swainson's Thrush	5.6	Wilson's Warbler	4.9
	Warbling Vireo	4.4	Wilson's Warbler	4.5	Mountain Chickadee	4.6
	MacGillivray's Warbler	4.1	Townsend's Warbler	4.3	Ruby-crowned Kinglet	4.1
	Mountain Chickadee	3.6	MacGillivray's Warbler	4.2	Varied Thrush	3.2
	Similar Species = 9		***Similar Species = 8***		***Similar Species = 5***	
BURNED	Dark-eyed Junco	15.8	Wilson's Warbler	17.0	Yellow-rumped Warbler	16.0
	Dusky Flycatcher	14.6	Warbling Vireo	13.6	Dark-eyed Junco	9.2
	Yellow-rumped Warbler	12.4	Yellow-rumped Warbler	11.5	Townsend's Warbler	7.6
	Wilson's Warbler	10.4	Dark-eyed Junco	9.7	Swainson's Thrush	6.6
	Pine Siskin	5.8	Swainson's Thrush	6.8	Warbling Vireo	6.0
	Orange-crowned Warbler	4.2	Orange-crowned Warbler	6.8	Cassin's Vireo	5.6
	Warbling Vireo	3.7	Townsend's Warbler	6.3	Pine Siskin	5.3
	MacGillivray's Warbler	3.3	MacGillivray's Warbler	2.8	Golden-crowned Kinglet	4.2
	Chipping Sparrow	3.1	Golden-crowned Kinglet	2.5	Chipping Sparrow	3.8
	Rufous Hummingbird	2.6	Townsend's Solitaire	2.4	Mountain Chickadee	3.7

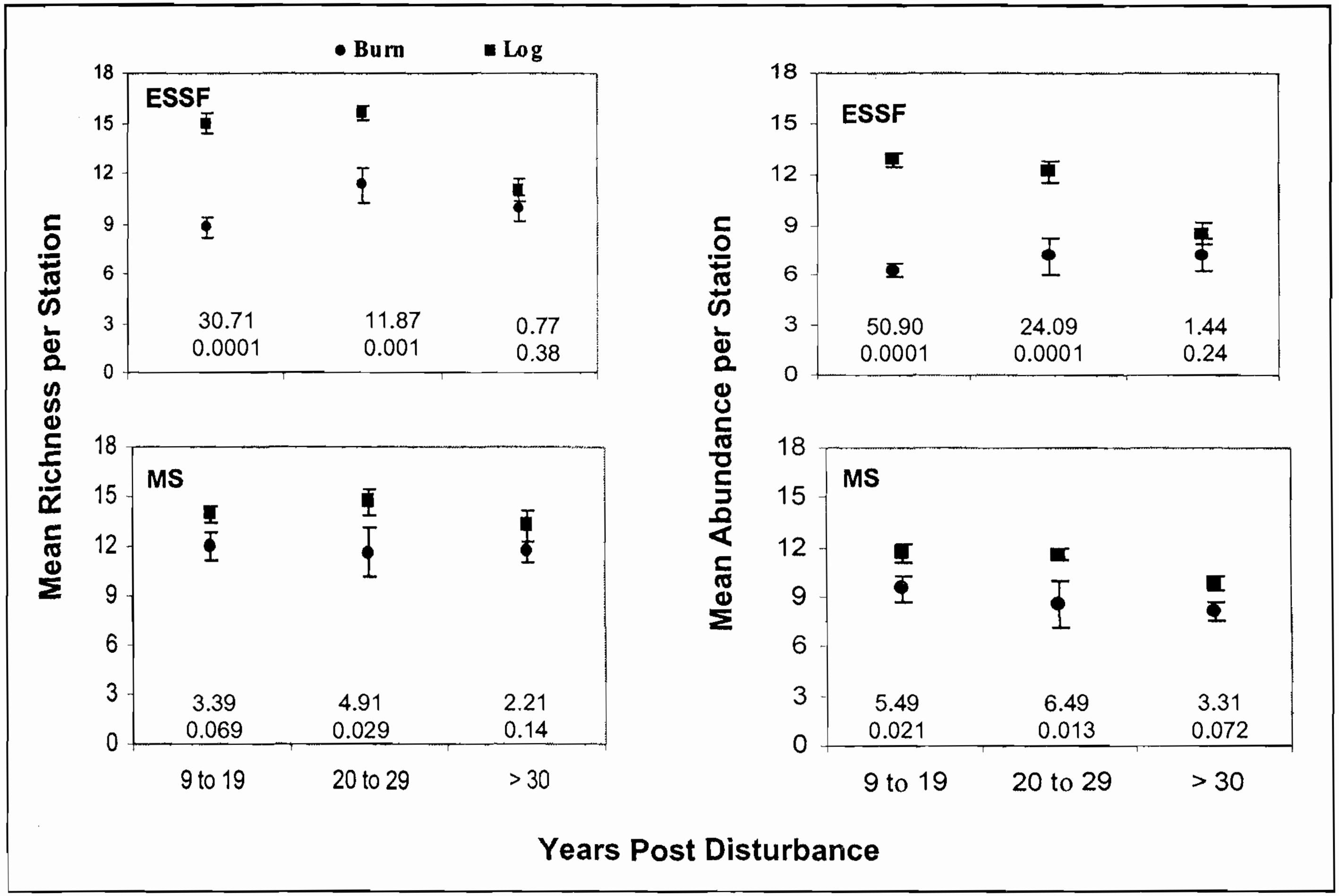


Figure 2.3 Mean songbird richness and abundance per station (± SE) for three age classes of time since disturbance. Results from ANOVA and orthogonal contrasts (F-value over p-value) for each age class above x-axis at each comparison.

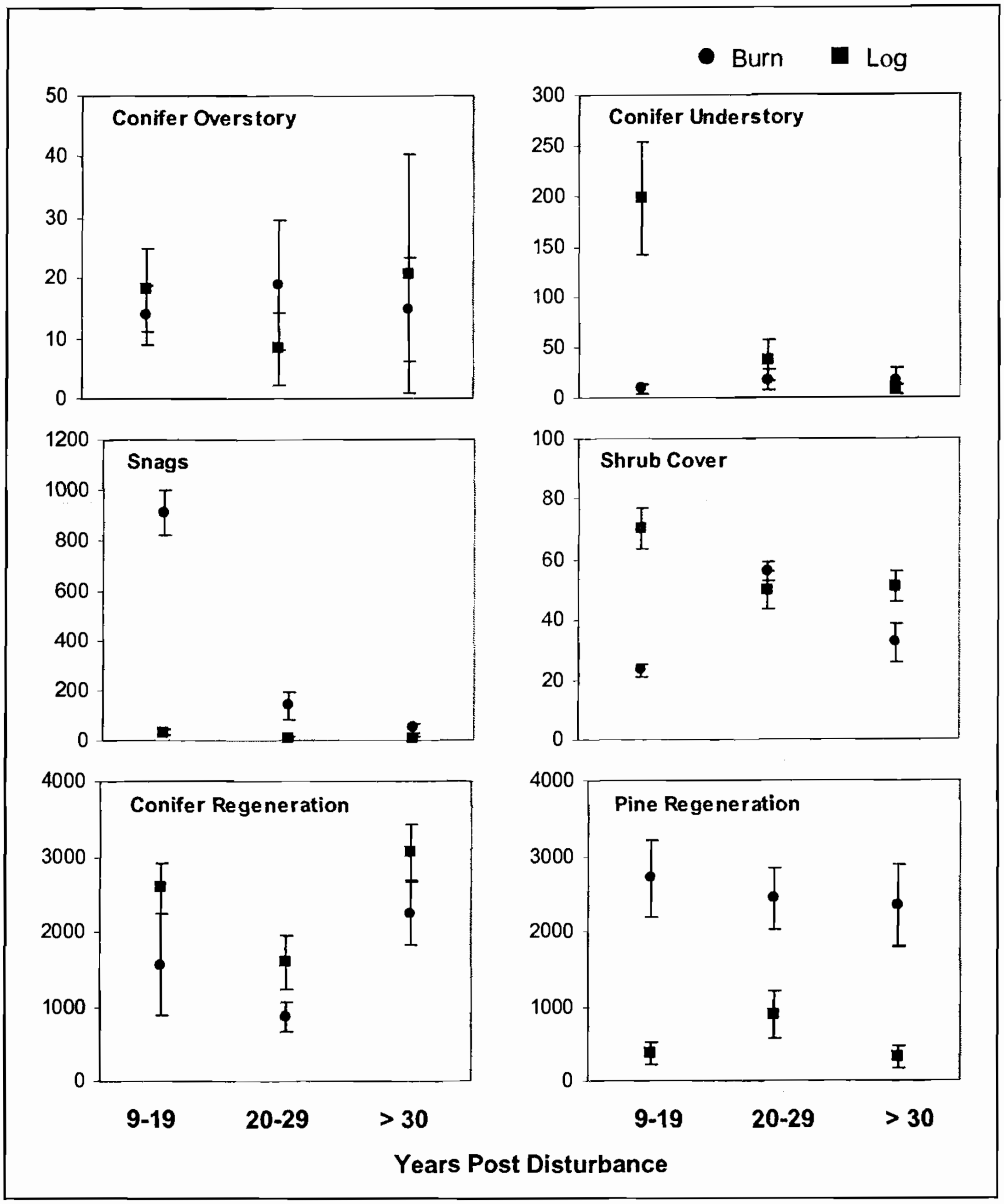


Figure 2.4 Mean stems per ha (mean percent for shrub cover, ± SE) at three different age classes for vegetation variables in the ESSF biogeoclimatic zone.

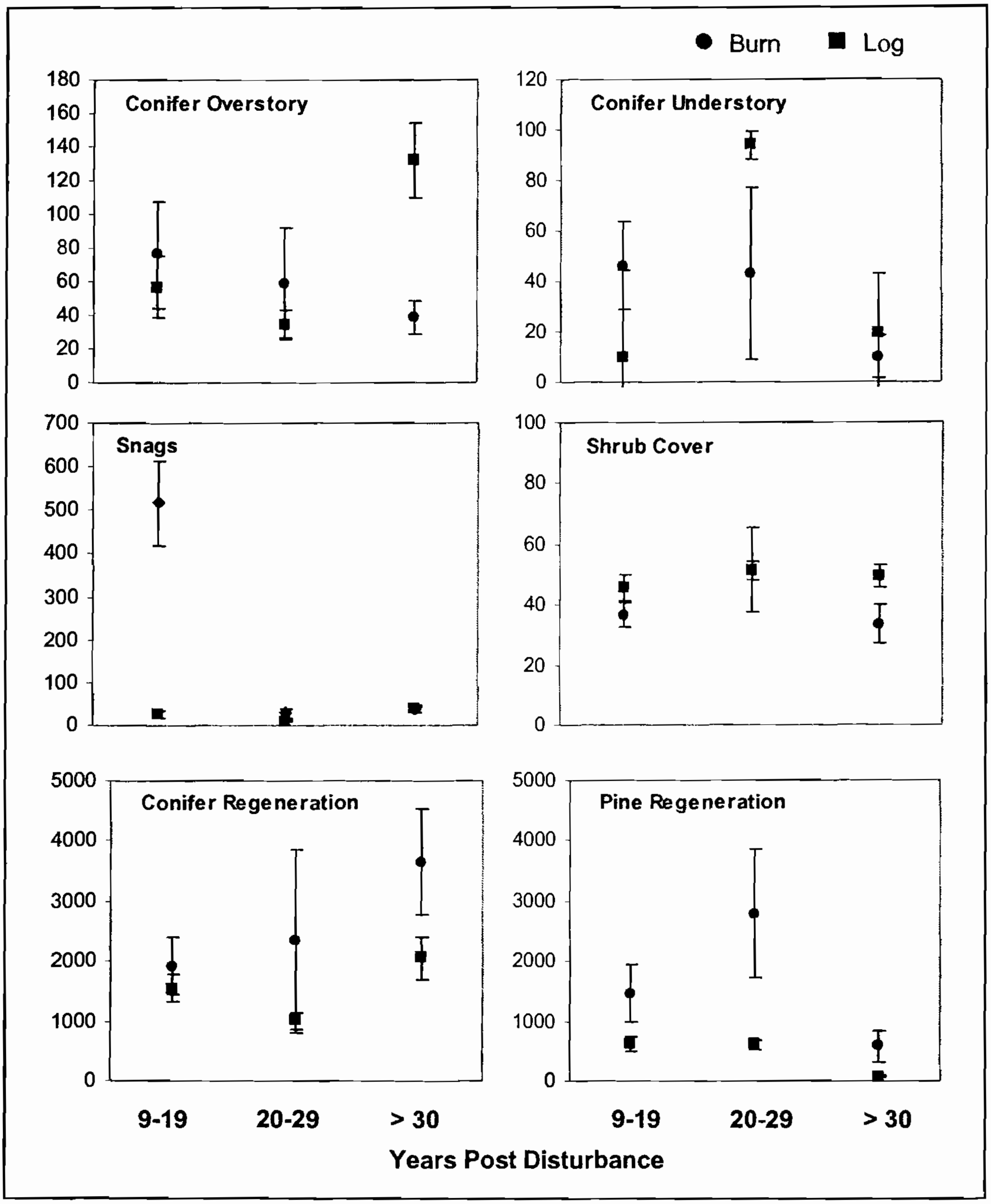


Figure 2.5 Mean stems per ha (mean percent for shrub cover, ± SE) at three different age classes for vegetation variables in the MS biogeoclimatic zone.

Discussion

This is the first study, to my knowledge, to compare songbird communities within post-harvest and post-wildfire stands in relation to residual trees outside the boreal mixedwood forest (Schieck and Hobson 2000). Results showed that although some species appear to respond differently to disturbance types in general the songbird communities in young burned and logged stands were similar, as evidenced by the similar dominant species, evenness, and diversity. With two exceptions, the same species occurred in both disturbance types. However, logged stands had higher mean richness and abundance than burned stands. This difference is likely related to differences in the vegetation between the two disturbance types. Logged stands had greater shrub cover and shrub richness, greater basal area of broadleaf trees, generally fewer regenerating trees, as well as a greater number of vertical vegetation layers.

Two of these vegetation features, shrubs and broadleaf trees, are key structural factors influencing the richness and abundance of vertebrates in Pacific Northwest forests (Bunnell et al. 1999). Broadleaf trees support a higher arthropod density than coniferous trees (Schimpf and MacMahon 1985), likely due to their relatively higher concentrations of foliar nitrogen (a limiting resource to many foliage-feeding arthropods; Waring and Cobb 1992) and the absence of thickened cuticles on their leaves (Jackson 1979), and thus provide greater foraging opportunities for foliage gleaning birds. Fallen leaves decompose readily, encouraging a rich arthropod fauna (Bunnell et al. 1999), and providing foraging opportunities for ground feeding insectivorous birds. In addition, because they are less resistant to decay than conifers, broadleaf trees provide cavity sites at younger ages, benefiting cavity-nesting birds (Raphael et al. 1987). Shrubs present both feeding (foliage gleaning and fruit eating) and nesting opportunities for birds. Many birds associated with early successional forest stands, including many of those found in this study, use shrubs as the supporting structure or as cover for their nests (Appendix A, Chapter 3). Not only was shrub cover higher in logged stands, but Sitka alder, which was the primary shrub species used for nesting in the study stands (Chapter 3), had greater mean cover in logged stands. Bird species diversity has also been shown to be positively related to the vertical heterogeneity in a stand (Willson 1974, MacArthur and MacArthur 1961). An increase in the number and volume of vegetative layers diversifies the niches available to birds, providing foraging and nesting habitat for more species.

Results from the five other published studies that have compared songbird communities in post-harvest to post-wildfire forest stands are variable. Imbeau et al. (1999) compared post-fire and post-harvest bird communities in boreal black spruce (*Picea mariana*) stands and found avian community composition, richness, and abundance to be similar between post-fire and post-logged stands of similar development stages, with the exception of the youngest stands (regeneration < 2 m tall), in which cavity nesting birds were more abundant in burned stands and neotropical migrants were more abundant in logged stands. In contrast, Schulte and Niemi (1998), reported overall richness and number of individuals to be higher in 2-yr. old burned forests than similar-aged logged forests in Minnesota. However, of the 71 species they examined, 60 had similar abundance between the two disturbance types, seven species were more abundant in burned stands and four were more abundant in logged stands. The six most abundant species were the same in both types, although nine species were unique to each disturbance type. They attributed these differences to greater heterogeneity of vegetation in burned forests and differences in the number of live and dead trees and amount of hazel (*Corylus cornuta*) in the shrub layer. Hobson and Schieck (1999), working in the boreal mixedwood forest of northern Alberta, found that bird abundance was higher in post-harvest stands than in post-fire stands. Differences between the bird communities in the disturbance types were large initially, but diminished as the time since disturbance increased from 2 to 28 yrs. However, when they considered residual tree patches as well as disturbance type and stand age they found species richness to be higher in post-fire than post-harvest stands and that bird communities differed between fire and logging within each age class (Schieck and Hobson 2000). Again, these differences diminished through time as the age of the stands increased. Hutto (1995) surveyed birds in recent (1-2 yr.) wildfires in the Rocky Mountains in Montana and compared his data to that from other studies in different habitats in the Rocky Mountains, including early successional logged stands. He found greater similarity between the bird communities in mid-successional (10-40 yr. old) post-harvest and post-fire stands than for early-successional (< 10 years old) post-harvest and post-fire stands.

Results from the above studies suggest that although bird communities in post-fire and post-harvest forest stands differ, differences are not great, with the exception of recently disturbed (< 5 yr.) stands, in which bird species that nest or forage in large snags are more prevalent in burned than logged stands, and open-country birds are more abundant in logged stands. Convergence through time is attributed to snags falling, which leads to fewer snag -nesting or -foraging species which are prevalent in early post-fire stands, and growth of trees, which leads to older stands being dominated by forest species rather than open parkland species (Hobson and Schieck 2000).

In my study, strong convergence of the bird communities was seen in the ESSF, but not in the MS, although snags declined markedly with time in both subzones. In the ESSF, most vegetation variables examined became more similar through time, with the exception of the density of regenerating pine. In contrast, in the MS, differences in the density of residual conifer overstory trees became greater through time, as did differences in the density of regenerating conifers. This is likely due to differences in the types of logging, rather than successional patterns. Whereas recently logged stands in the MS were generally clear-cuts with scattered residuals, similar to the recent severe burns, older cutblocks in the MS had high densities of residuals, often including large-diameter canopy trees, resulting from early high-grade logging. These stands were very diverse, with many layers of trees. Conversely, older burns were relatively homogenous, dominated by high densities of pole-sized stems and were generally less structurally diverse. It has been suggested that increasing the density and size distribution of residual trees likely decreases the time to convergence between wildfire and logging (Lee et al. 1999). In this system, at least, this was not the case for bird communities.

The Influence of Residual Trees

There was a strong association between density of residual trees and the abundance of individual bird species, as evidenced by the fact that residual trees entered into 22 of 24 models in the MS and 12 of 20 models in the ESSF. The most consistent association was with broadleaf trees, which was positive for all species with the exception of the Yellow-rumped Warbler, likely reflecting a preference for coniferous forests by this species (Campbell et al. 2001). Species most strongly associated with broadleaf trees included Black-capped Chickadee, Dusky Flycatcher, Warbling Vireo, and Red-naped Sapsucker. These species all nest in cavities or crowns of broadleaf trees, and have been identified as deciduous associates in other studies (e.g., Hutto and Young 1999, Hagar et al. 1995). Broadleaf trees were also the only residual tree variable to significantly influence overall bird richness and abundance, likely due to higher arthropod densities and greater bole decay. Broadleaf trees have been identified as one of the most important structural features influencing vertebrate species richness in Pacific Northwest forests (Bunnell et al. 1999). Huff and Raley (1991) found the strongest positive association between total bird abundance or richness and stand structure was with live deciduous tree characteristics such as density and basal area.

Residual conifer overstory trees were strongly associated with 16 of the 24 species tested in the MS, nine positively and seven negatively. The species relationships are generally consistent with those revealed in previous studies and are interpretable based on the natural history of the species. Species negatively associated with increasing densities of residual overstory trees were generally those that feed or nest on or near the ground in open habitats, such as the Dark-eyed Junco, American Robin, and MacGillivray's Warbler. These species have previously been reported to be negatively associated with tree density in Pacific Northwest Forests (Marcot 1984, Hansen et al. 1995b). Species with the strongest positive responses were a mix of those preferring open forest stands with large trees in the canopy (Western Tanager and Cassin's Vireo) and those preferring older closed-canopy forests (Townsend's Warbler and Golden-crowned Kinglet). All nest (Appendix A) and forage in trees (Ehrlich et al. 1988). Previous studies in other geographic regions and forest types have also found bird species associated with mature and old forest to increase in abundance with residual tree density and those species associated with open country and shrubby areas to decrease with residual tree density (Annand and Thompson 1997, Schieck et al. 2000, Hansen et al. 1995b). Although there were too few detections of Brown Creeper for analysis, the only logged stands where it occurred in this study were stands > 30 years post-disturbance in which patches of large diameter (> 60 cm dbh) western larch and Douglas-fir were retained post-harvest. The heavily furrowed bark of old-growth Douglas-fir has been postulated to harbor an abundant arthropod fauna that serves as food for Brown Creepers (Mariani 1987), and Weikel and Hayes (1999) found that Brown Creepers selected foraging trees in relation to the depth of furrows in the bark.

Although conifer overstory trees entered into fewer species models in the ESSF than in the MS, all associations with them were positive. The difference in response between subzones is likely due to the lower abundance of residual overstory conifer trees in the ESSF (averaging 5/ha in the ESSF vs. 55/ha in the MS, Table 2.1). Fewer single overstory trees are left post-harvest in the ESSF because there are fewer western larch and Douglas-fir trees. The dominant tree species in the ESSF, Engelmann spruce and subalpine fir, both have shallow root systems and tend to blow over if left singly, particularly on steep slopes. Wildfire similarly leaves few residuals of these species, as both are thin-barked trees that rarely survive fire (Stuart-Smith and Hendry 1998).

Conversely, residual conifer understory trees played a more significant role in the ESSF than in the MS, possibly because their abundance was greater in logged stands in the ESSF. The abundance of many bird species was positively associated with residual conifer understory trees, including Dark-eyed Junco, Wilson's Warbler, Swainson's Thrush, Chipping Sparrow, Olive-sided Flycatcher, Townsend's Warbler, Mountain Chickadee, and Pine Siskin. Several of these species were observed feeding on arthropod adults or larvae found on the needles of young Douglas-fir, subalpine fir and Engelmann spruce, and flying long distances (> 50m) across clearcuts to feed in patches of these trees. Some of the trees within these clumps were suppressed, or had been damaged by machinery during logging (pers. obs.). Subdominant trees are less vigorous and more susceptible to being attacked by foliage–feeding insects than dominant trees (Barbosa and Wagner 1989), and it could be that the residual trees had higher arthropod densities than the regenerating trees. Several bird species were also found to nest within clumps of residual conifer understory trees (e.g., Swainson's Thrush, American Robin, Yellow-rumped Warbler; unpubl. data). The denser foliage of the residual tree species appeared to provide better cover and support for nests than that of the regenerating pine trees.

Individual Species Response to Disturbance

Six species showed higher abundance in burned stands than logged stands: Cassin's Vireo, Northern Flicker, Red-breasted Nuthatch, Townsend's Solitaire, Western Tanager, and Yellow-rumped Warbler. Two of these, Northern Flicker and Red-breasted Nuthatch, are cavity nesting species, and it is likely that nesting sites within logged areas were less available than in burned stands given the substantially lower numbers of snags. Townsend's Solitaire nests on the ground, often under cover of logs or stumps (Bowen 1997) or in the root wads of upturned trees (pers. obs.), which are more prevalent in burned areas. Four of the above species, the Red-breasted Nuthatch, Western Tanager, Cassin's Vireo, and Yellow-rumped Warbler, were found by Hutto and Young (1999) to be relatively common in partially cut stands, but their abundance dropped strongly with increasing amount of timber removed. I suspect that the retention levels in the logged stands in my study were not high enough to provide good habitat for these species. Alternatively, the higher cover of shrubs in logged stands may play a role, because at least one species, the Western Tanager, prefers woodlands with little shrub development in the understory (Hudon 1999). If wildfires continue to be suppressed or if burned stands are salvage-logged after wildfire, it is possible that the above six species could decline throughout managed forests in the area. However, none of these species are confined to post-burn habitats, and only one, the Northern Flicker, reaches its highest abundance in post-fire stands (Hutto and Young 1999). Thus, differences in abundance between post-fire and post-harvest stands may not have significant implications for populations of these species.

Given the importance of dead and dying trees to cavity-nesting birds (e.g., Raphael and White 1984, Thomas et al. 1979), I expected that the lower snags densities in logged stands would result in a lower abundance of cavity-nesting birds in these stands. However, no clear pattern emerged. Of the five cavity-nesting birds with adequate abundance to conduct multiple regression analysis, only the Red-breasted Nuthatch and the Northern Flicker had significantly higher abundance in burns, and for the Northern Flicker this was only true in the ESSF and not the MS. The three other cavity-nesters tested (Mountain Chickadee, Black-capped Chickadee, and Red-naped Sapsucker) had either higher abundance in logged stands or showed no difference between disturbance types.

The lack of strong response by cavity-nesters seen in this study could be due to at least four reasons. First, the five species examined either prefer to excavate cavities in deciduous trees (Mountain Chickadee, Black-capped Chickadee, Red-naped Sapsucker and Northern Flicker; Campbell et al. 1997) or will nest in broadleaf trees as well as conifers (Red-breasted Nuthatch; Steeger and Hitchcock 1998). Logged stands had greater basal area of broadleaf trees than burned stands. Second, cavity sites may not have been limiting in logged stands. As above, this may relate to the greater abundance of broadleaf trees in logged stands. Although broadleaf trees may not be used for nesting or foraging by all cavity-nesters (e.g., Brown Creeper, Weikel and Hayes 1999), they may be able to compensate in part for the lower numbers of coniferous snags in logged stands. Third, most woodpeckers were not analyzed in this study. Other studies have identified Black-backed Woodpecker and Three-toed Woodpecker as species for whom habitat losses caused by forestry may be permanent (Imbeau 1999). Hunter (1992) and Wiens (1994) argued that it is these types of resident habitat specialists, often with large home range requirements, that are likely to be most sensitive to large scale habitat alterations occurring through forest management. Fourth, no recent (<5 years old) burns were included in my study. Hobson and Schieck (1999) found birds that nest or forage in large snags (e.g., Northern Flicker, Black-backed Woodpecker) had lower densities 15 and 30 yr. post-fire than 2 years post-fire. For Black-backed Woodpecker, the 1-3 years immediately following the fire have been identified as providing critical habitat for this species (Hutto 1995). Thus, the time period when woodpeckers would have been most likely to show differences was missed in this study, due to the fire history of the area.

Effects of Elevation

There was a strong negative association between elevation and richness, overall abundance, and abundance of all species tested except the Hermit Thrush. Although Townsend's Warbler and Wilson's Warbler showed positive associations with elevation in the MS, they showed an opposite response in the ESSF, suggesting preference for mid- rather than high elevations. Effects were particularly pronounced for species whose abundance was extremely low in the ESSF such as the Western Tanager and Cassin's Vireo, and for species strongly associated with the density of broadleaf trees such as Red-breasted Sapsucker and Black-capped Chickadee. Medin et al. (2000), who surveyed birds along an elevational gradient from shadscale (1500m) to alpine (3300m) in the Great Basin, found bird species richness and abundance to follow a parabolic curve, peaking at upper mid-elevations, and declining at higher and lower elevations. However, the results of Medin et al. (2000) are confounded by vegetation structure, which was also most complex at upper mid-elevations. Based on the lack of a relationship between the number of vegetation layers and elevation (unpubl. data) in my study, I speculate that the decline in songbird abundance and richness with elevation primarily reflects a declining gradient of overall productivity, resulting from the shorter snow-free season and colder temperatures at higher elevations.

Scope and Context of the Study

The random stratified design used in this study allows statistical inference to all stands included in the pool of potentially selected stands within the study area. This includes all logged or burned stands in the MS and ESSF, between 5-45 years-since-disturbance. Because the study area did not include any recent (< 5 yrs.) wildfires, the period immediately following disturbance could not be examined. Practically, the geographical scope likely extends outside the study area to young logged and burned stands in the MS and ESSF in the northern Rocky Mountains. Application of the results to other biogeoclimatic zones or areas outside the northern Rocky Mountains should be done with caution. The habitat use of individual species can vary widely, even within regions (e.g., Hansen et al. 1995b) and hypotheses about factors controlling species diversity cannot be generalized to all locations (Hansen and Urban 1992).

Because this was not a manipulative study, bird-habitat relationships presented here do not necessarily reflect causal relationships and may be affected by other variables not examined in the analysis. These include stand-level variables such as shrub cover, snags, or down wood, and landscape level variables such as stand size, forest types surrounding stands, or the distance of stands from mature forest. Adding these variables to the models would likely increase the amount of variation explained by them, and offer greater predictive power.

In addition, only common species, or those occurring at more than 2/3 of the point count stations, were analyzed. Rare species may be more sensitive to the differences in vegetation structure between disturbance types.

Finally, the reproductive success of birds was not examined in this study. Bird abundance may not reflect habitat quality in all areas (Van Horne 1983, Vickery et al. 1992a). Chapter 3 addresses this issue, examining nest success in burned and logged stands in relation to the density of residual trees.

Conclusions and Management Recommendations

Clearly, logging does not mimic wildfire in terms of vegetation. Burned stands had greater numbers of snags, down wood, and regenerating trees, whereas logged stands had greater basal area of deciduous trees, higher density of residual conifer understory trees, greater cover and richness of shrubs, and more complex vertical structure. Despite these structural differences, burned and logged stands had relatively similar songbird communities. Differences between disturbance types were mainly in terms of relative abundance rather than in the presence or absence of species. The higher overall richness and abundance of birds in logged stands was associated with vegetative features less abundant in wildfires, such as deciduous trees and residual conifer understory trees.

Thus, past logging practices in my study area either benefited or did not negatively influence most common early seral songbirds in the study areas. This is likely related to the fact that very few of the stands in my study area were intensively managed at the time of this study; hence they had relatively complex vegetation structure. More intensive management resulting in fewer residual trees, deciduous trees, pieces of down wood, and less shrub cover would likely create very different habitat (e.g., Hansen et al. 1991) and produce different results. Past logging practices did not benefit all species of songbirds, however. Expanding forest management practices in the study so that they more closely emulate wildfire may be important for those six species of birds whose abundance was higher in burned stands than in logged stands. This could be done by increasing the number of snags and expanding the upper range of residual tree densities and basal area in logged stands.

One of the most significant differences between logged and burned stands was the difference in the number of snags. Standing dead trees were almost completely absent from the logged stands in this study. Two of the six species with lower relative abundance in logged stands (Northern Flicker and Red-breasted Nuthatch) were cavity-nesters. Increasing the number of snags left in harvested areas should benefit these species, as well as other species that nest and forage in dead trees that were not examined in this study (e.g., Hairy Woodpecker, Brown Creeper, Pileated Woodpecker). Cavity-nesting species using live broadleaf trees, such as the Red-naped Sapsucker and Black-capped Chickadee, showed either higher or similar abundance in logged stands relative to burned stands, and are likely not of great management concern providing broadleaf trees are maintained within harvested areas. The species and diameter classes of conifer snags most likely to have cavities in them were western larch and Douglas-fir of at least 20 cm dbh and averaging 40 cm dbh and greater than 5 m tall (unpubl. data). I recommend these types of snags be left where possible. Western larch and Douglas-fir are wind-firm, long-lived species, and will provide long-lived snags. Species such as Douglas-fir also decay ‘from the outside in’ (Cline et al. 1980), and are thus also favorable to weaker excavators such as nuthatches and chickadees (Steeger and Hitchcock 1998). This recommendation is similar to that from other researchers, who have found that, in general, the taller and larger diameter snags are more likely to be used by woodpeckers (Weikel and Hayes 1999, Bull et al. 1992), as well as other vertebrate species (see references within Bunnell et al. 1999).

Second, higher densities of large residual conifer overstory trees than found in this study should be retained in some stands throughout the landscape, in order to provide good habitat for birds associated with open forest stands. In this study, the mean density of overstory conifers was relatively high (55/ha in the MS, Table 2.1) but the basal area (mean

4.4 m^3/ha in the MS) and median diameter class (19-27 cm dbh) were low. Considering that stand volumes in the study area currently average 250 m^3/ha, and harvested tree diameter averages approximately 30 cm (D. Braybrook, Tembec Industries, BC, pers. comm.), most residual trees were likely sub-dominant or sub-canopy trees. Species such as Western Tanager and Cassin's Vireo that reached higher abundance in burned than logged stands were typically found in burned stands with high numbers of large diameter (> 35 cm) Douglas-fir and western larch residual trees. Thus, leaving greater densities of large residual trees in logged stands should provide better habitat for these species.

The influence of residual tree density on the growth and yield of the regenerating stand will also be a consideration in determining what range of residual tree densities to retain. Studies have shown that, above certain densities, residual trees can have a negative influence on the regenerating stand (Acker et al. 1998, Rose and Muir 1997). In some cases, trade-offs may have to be made between wood production and bird diversity.

No one single silvicultural treatment or management regime applied throughout the landscape will provide good habitat for all species of forest birds. Some species were positively associated with the density of residual trees, others negatively, indicating that a range of residual tree densities and types throughout the landscape is needed to provide good habitat for a variety of species. Of the residual tree types examined, broadleaf trees were most strongly associated with total bird abundance and richness. Retaining these in managed stands should be a priority, as even small numbers of them increased songbird richness and abundance. The potential implications of reducing broadleaf trees are apparent in Scandinavia, where intensive forest management has diminished the density of deciduous trees and a large portion of the species listed as endangered are associated with hardwoods (Bernes 1994). This recommendation is consistent with that of other ecologists who are recommending broadleaf trees be restored or maintained in managed forests (Bunnell et al. 1999, Weikel and Hayes 1999, Angelstam and Mikusinski 1994).

The density of residual conifer understory trees was associated with the abundance of many species, particularly in the ESSF. Retaining residual understory trees in logged stands at higher elevations should increase songbird richness and abundance in these stands. Although this study did not examine the spatial distribution of residuals, clumps of healthy residual understory trees with high canopy cover appeared to receive greater foraging and nesting use than single scattered trees (pers. obs.), while single scattered trees were used as song posts.

The density of residual overstory conifer trees was strongly associated with the abundance of many species, particularly in the MS. As species associations were both positive and negative, a variety of residual tree densities should be left throughout the landscape to provide good habitat for a variety of songbird species. Although this study did not examine the optimal distribution of residual tree densities among stands throughout the landscape to maximize habitat value for songbird populations, the data do provide a foundation for models to address this question. The range of residual trees densities in this study, 0-320/ha in the MS and 0-119/ha in the ESSF, included densities high enough to provide some habitat for birds typically associated with mature forest, such as Golden-crowned Kinglet. However, as mentioned, higher densities or greater basal area of residual trees will likely be required to provide habitat for species preferring open forest stands. The overstory residual conifer trees in this study were almost entirely western larch, Douglas-fir, and white or Engelmann spruce. Residual tree-bird habitat relationships may differ for other tree species such as lodgepole pine.

Residual trees should not be relied upon to provide all habitat requirements for mature forest species immediately following harvest. Despite observations of Townsend's Warbler and Golden-crowned Kinglet foraging in recently logged stands (< 10 yr.) with residual trees, I found no evidence they nested in these stands (although there was evidence they nested in stands logged > 30 years ago with high densities of residuals, unpubl. data). The highest densities of these two species occur in mature or old stands (Davis et al. 1999), and their presence in recently logged stands was likely dependent on the mature forest surrounding the cutblocks. If these mature stands are cut before the previously harvested stands have developed enough to supply nesting habitat, these species will likely disappear from young stands. Further, some species associated with old forest, such as Varied Thrush and Brown Creeper, were rarely detected in this study. Since these species are moderately common in old forests in my study area (unpubl. data), this suggests residual tree densities were not high enough to provide adequate habitat for these species, or that these species require aspects of mature and old stands not found in young stands with residuals. Thus, stands of mature and old trees should also be left to provide habitat for these species.

Leaving residual trees emulates only one characteristic of wildfire. Without considering the rate-of-return of disturbance and the associated seral stage distribution throughout the landscape, or the size and spatial distribution of disturbance, efforts to maintain biodiversity in managed forests are unlikely to be successful.

THE INFLUENCE OF RESIDUAL TREE DENSITY AND DISTURBANCE TYPE ON NEST PREDATION IN GROUND- AND SHRUB-NESTING SONGBIRDS

Introduction

Predation is the main cause of nest failure in most temperate landbird communities. Accounting for an average of 80 % of the nest losses of open-cup nesting birds (Martin 1993a, Martin 1992, Ricklefs 1969), nest predation is thought to be a powerful force shaping many aspects of avian reproductive ecology and life history (e.g., Sieving and Willson 1998, Martin 1993b, 1988, Slagsvold 1982). Increased nest predation resulting from forest fragmentation has been proposed to be a primary cause of declines in populations of migratory songbirds in North America (Terborgh 1989, Wilcove 1985). This hypothesis prompted numerous studies examining nest predation in relation to size of forest patches (Leimgruber et al. 1994, Nour et al. 1993, Andrén and Angelstam 1988, Small and Hunter 1988, Wilcove 1985), forest edges (Song and Hannon 1999, Cotterill and Hannon 1999, Fenske-Crawford and Niemi 1997, Paton 1994, Rudnicky and Hunter 1993, Andrén and Angelstam 1988, Yahner and Scott 1988, Angelstam 1986), and amount of forest cover in the landscape (Hartley and Hunter 1998, Robinson et al. 1995). The general pattern emerging from these studies is that nest predation is often higher near forest edges in agricultural or rural landscapes, but does not appear to be higher along edges in forested landscapes with little human settlement, likely due to lower numbers of generalist predators such as American Crow (*Corvus brachyrhyncos*), raccoon (*Procyon lotor*) and skunks (*Mephitis* spp.) in these areas.

In forested landscapes, stand-level forest management practices may affect nest predation more than patch size or edge effects. Silvicultural practices can alter the species composition, distribution, and cover of vegetation in young stands relative to naturally disturbed stands (Chapter 2, Hansen et al. 1991), potentially altering habitat and search efficiency of nest predators (Martin 1993b). Leaving varying densities of residual (green) trees and snags within harvested areas is emerging as a major strategy for integrating ecological and economic objectives of forest management in temperate forests (Franklin et al. 1997, Hansen et al. 1995a). Known as variable or green-tree retention, this practice is thought to make harvested areas more closely resemble those created by natural disturbances, reducing the impacts of forest harvest on wildlife. Recent studies have shown that leaving patches of trees within cutblocks can increase abundance and richness of birds relative to levels in clear-cuts in aspen-dominated (Schieck et al. 2000, Merrill et al. 1998, Norton and Hannon 1997), and conifer-dominated (Seip and Parker 1997, Hansen et al. 1995b, Chapter 2) forests. However, none of these studies examined nest predation.

Retaining trees in harvested areas could increase predation on songbirds by providing perches for avian predators, enabling them to be more successful predators (Yahner and Wright 1985), or by providing habitat or facilitating travel through harvested areas for nest predators such as red squirrels (*Tamiasciurus hudsonicus,* Tittler and Hannon 2000). The results of Vega (1993) in the Pacific Northwest support this hypothesis. She found greater predation of artificial nests placed in shrubs in stands with green-tree retention (4-13 green trees/ha) than of those placed in clear-cuts or mature forest stands. Studies examining partial cuts or higher levels of retention, however, have not documented similar effects. Tittler and Hannon (2000) reported no difference in nest predation on artificial nests among moderate retention (48-55 trees/ha), high retention (86-133 trees/ha), or mature forest stands (246-414 trees/ha) in aspen-dominated boreal mixedwood forest. Similarly, Steventon et al. (1999) found no difference in nest predation among clearcuts, 30 % removal, 60 % removal, and mature coniferous forest stands in northwestern British Columbia. Thus, the effects of variable retention harvesting on nest predation are unclear, and may depend on the amount of trees retained and forest type.

There are few other studies of the effects of different harvest practices on nest predation, and these mainly compare clearcuts and mature forest, providing little insight as to the influence of variable tree retention on nest predation. Lower rates of nest predation in clearcuts than in mature forest were reported in Maine by Rudnicky and Hunter (1993) and in boreal Quebec by Darveau et al. (1997). In contrast, there was no significant difference in nest predation between clearcuts and forests (DeGraaf and Angelstam 1993), or among mature forest, shelterwood cuts, and clearcuts (King and DeGraaf 2000) in New Hampshire, and very small differences (< 10 %) between clearcuts and forests in Pennsylvania (Yahner and Cypher 1987). Differences in the results between Maine and Quebec vs. New Hampshire and Pennsylvania may be due to differences in the predator communities, levels of human activity, and dominant vegetation type (coniferous vs. deciduous, Darveau et al. 1997). However, examining the correlates of vegetation variables with nest predation from studies conducted in mature forest suggests that greater canopy cover (Tittler and Hannon 2000, Hanski et al. 1996), greater tree density (Rangen et al. 1999), greater conifer basal area (King et al. 1998), higher subcanopy height, greater conifer cover and greater green cover (Song and Hannon 1999), and the presence of coniferous forest understory and coniferous forest (Sieving and Willson 1998) may all increase risk of nest predation on artificial nests. Combined, these results imply that nest predation should increase with residual tree density, particularly conifer tree density. If this is the case, stands with green-tree retention may act as sinks (Pulliam 1988) or ecological traps for songbirds in forested landscapes (Vega 1993, Bunnell et al. 1999). As variable retention harvesting increasingly replaces clear-cutting, determining if this practice increases nest predation for forest songbirds is important.

Quantifying nest predation is confounded by the difficulty in locating natural nests and determining their fate. Artificial nests are widely used to assess the effects of different variables on nest predation because their ease of use facilitates stronger experimental designs and greater sample sizes than is possible using natural nests (Major and Kendall 1996). Studies using artificial nests have had a strong influence on ecological theory and conservation by providing the main experimental evidence to conclude that fragmentation of forests in eastern North American increases rates of nest predation (e.g., Robinson et al. 1995, Small and Hunter 1988, Wilcove 1985). Although it is widely acknowledged that absolute rates of predation on artificial nests often do not match those on natural nests, many researchers argue that patterns or relative rates of predation on artificial nests are similar to those on natural nests over time, among sites, or between different habitat types (Tittler and Hannon 2000, Cotterill and Hannon 1999, Bayne and Hobson 1997, Darveau et al. 1997, Andrén and Angelstam 1988). However, few studies have compared patterns of predation on natural and artificial nests, and those that have report conflicting results (Davison and Bollinger 2000, King et al. 1999, Major and Kendall 1996). Potential causes of this difference include the frequent use of unrealistic looking wicker baskets for nests (Davison and Bollinger 2000), deployment of nests in different densities, spacing, or microhabitats than natural nests (Major and Kendall 1996), nest defense by adults at natural nests (Montgomerie and Weatherhead 1988), and use of Japanese Quail (*Coturnix corturnix*) eggs, which are much larger and have thicker eggshells than typical songbird eggs (Haskell 1995a). Small mammals, such as *Peromyscus,* cannot open Japanese Quail eggs (DeGraaf and Maier 1996, Haskell 1995a, Roper 1992) so unless scratches on the eggs are interpreted as predation events, predation pressure by small mammals may be underestimated and comparisons of nest predation among habitats differing in small mammal abundance or distribution may be misleading. In addition to real eggs, use of plasticine eggs (Cotterill and Hannon 1999, Bayne et al. 1997, Darveau et al. 1997), which are easily marked and permit the identification of the various classes of predators, may help reduce this bias. However, given the ubiquity of artificial nests studies and their influence on ecological theory and conservation, the assumptions of these studies should be examined critically (Davison and Bollinger 2000) and artificial nest studies corroborated with studies of natural nests where possible.

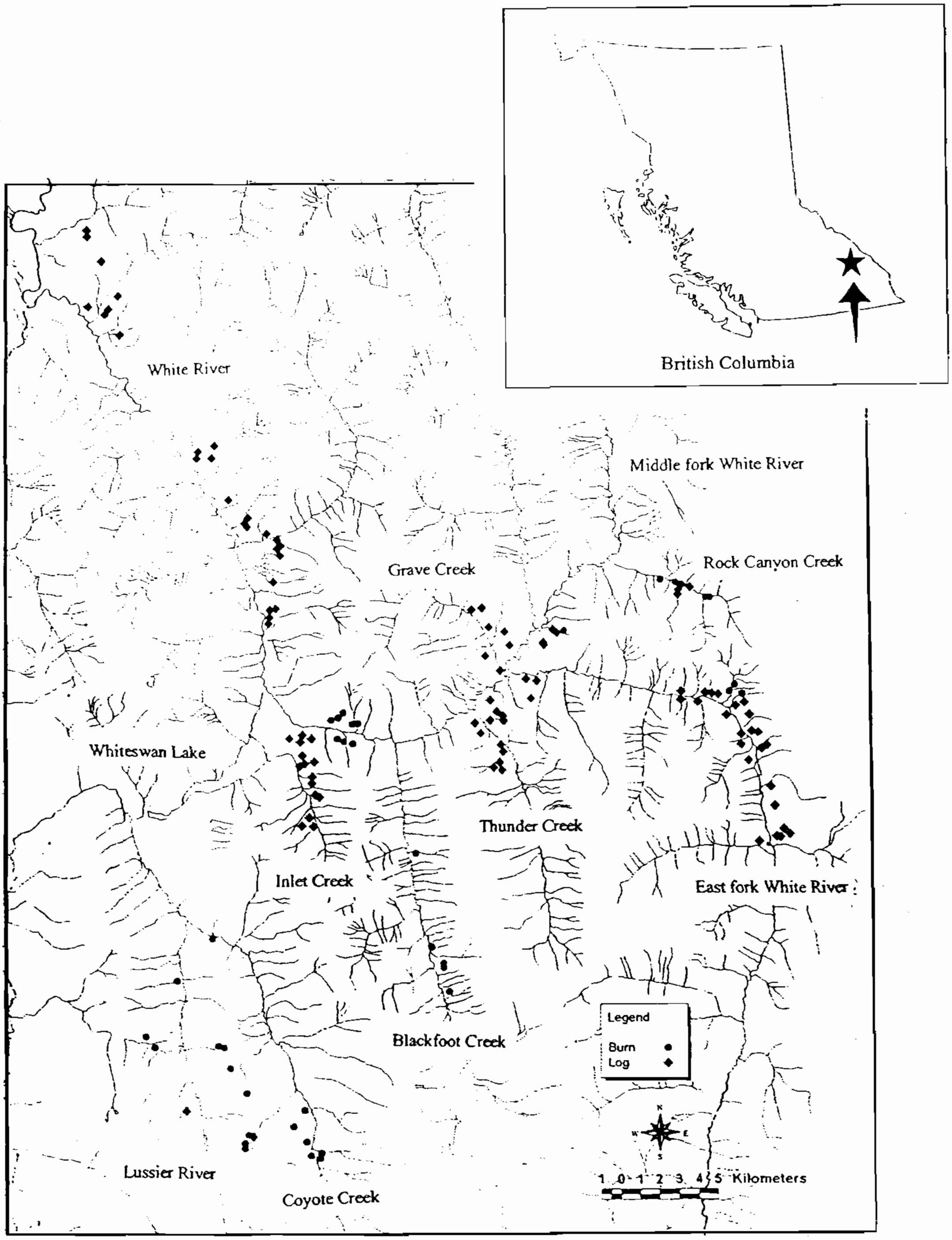
This study was designed to examine the effects of variable densities of residual trees on predation on songbirds nests using both experimental (artificial nests) and observational (natural nests) approaches. Most artificial nest studies use mature forest stands as controls for harvested areas (e.g. Tittler and Hannon 2000, King and DeGraaf 2000, Rudnicky and Hunter 1993). In this study, I used stands burned by wildfire of similar age as controls, based on the idea that forest practices that emulate naturally disturbed stands should maintain biodiversity (Swanson et al. 1993, Hunter 1993). My four primary objectives were 1) to test the hypothesis that predation on songbird nests is positively related to the density of residual trees in a stand, 2) to test the hypothesis that there is no difference in the amount of nest predation between logged and burned stands of similar ages, 3) to determine the major nest predators in the study area, and 4) to determine whether the patterns of predation on artificial nests were similar to those on natural nests.

Methods

Study Area

This study was conducted in the Rocky Mountains of southeastern British Columbia in the White and Lussier watersheds (49°54' - 50°24' N, 115°36' -115°06' W, Figure 3.1). The area includes forests managed for timber production and covers approximately 100,000 ha within the Dry Cool Montane Spruce (MSdk) and the Dry Cool Engelmann Spruce-Subalpine Fir (ESSFdk) biogeoclimatic subzones (Braumandl and Curran 1992). The MSdk (hereafter MS) occurs from 1200 to 1650 m in elevation on south aspects and 1100 to 1550 m on north aspects and is dominated by interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), white spruce (*Picea glauca*), and western larch (*Larix occidentalis*).

Figure 3.1 Location of point count stations within the study area, Canadian Rocky Mountains, British Columbia, Canada. Artificial and natural nest stands were located within Grave Ck, Thunder Ck, Blackfoot Ck, Lussier River, East Fork White River and Middle Fork White River.



Extensive seral stands of lodgepole pine (*Pinus contorta* var. *latifolia*) are common due to widespread fires, and trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) are also present, particularly at lower elevations. Understory vegetation is dominated by buffaloberry (*Sheperdia canadensis*), Utah honeysuckle (*Lonicera utahensis*), Sitka alder (*Alnus crispa sinuata),* common juniper (*Juniperus communis*), Oregon grape (*Mahonia aquifolium*), and pinegrass (*Calamagrostis rubescens*). The ESSFdk subzone (hereafter ESSF) ranges from 1650 to 2100 m on south aspects and 1550 to 2050 m on north aspects and is dominated by Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Seral stands of lodgepole pine are common, but aspen and birch occur rarely. False azalea (*Menziesia ferruginea*) dominates the shrub layer, with lesser amounts of black huckleberry (*Vaccinium ovalifolium*) and white-flowered rhododendron (*Rhododendron albiflorum*). The climate in both zones is characterized by warm dry summers and cold winters. Snowfall varies with elevation, increasing substantially at higher elevations in the ESSF.

The primary potential nest predators in the study area include red squirrel, golden-mantled ground squirrel (*Spermophilus lateralis*), Columbia ground squirrel (*Spermophilus columbianus*), yellow pine chipmunk (*Eutamius amoenus*), least chipmunk (*Eutamius minimus*), deer mouse (*Peromyscus maniculatus*), red-backed vole (*Clethrionomys gapperi*), Common Raven (*Corvus corax*), Gray Jay (*Perisoreus canadensis*), and Steller's Jay (*Cyanocitta stelleri*).

Artificial Nest Experiment

The artificial nest experiment included 24 stands, 16 logged and 8 burned, based on the criteria that they cover a range of residual tree densities (0 – 180 trees/ha), were disturbed 10–20 years ago, were mid-elevation (1300-1700 m) and at least 10 ha in size, and were accessible within a one hour drive from the field camp. These stands were chosen from a pool of 176 randomly selected stands in the study area established as part of another study (Chapter 2). The year before the current study began, the number of residual trees in each of the 176 stands was quantified in four 0.1256 ha vegetation sampling plots, one centered on a point count station located near the center of the stand, and three others centered 60 m from the point center at 0°, 120°, and 240°. Within each plot, residual trees were tallied by species and diameter class (3-11, 11-19, 19-27, 27-35, 35-43, > 43 cm diameter breast height). From these data, the density of residual trees > 19 cm diameter (dbh) was calculated.

Artificial grass nests (10 cm x 4 cm; Mangelsen's, Omaha, Nebraska), each baited with one plasticine egg and one Chinese Painted Quail (*Coturnix chinensis*) egg, were used to assess relative rates of nest predation among stands. Plasticine eggs were used to aid in predator identification from marks left in the plasticine (Moller 1987). Plasticine eggs were painted with non-toxic paint, shaped to resemble quail eggs, and wired to the bottom of the nest so that they could not easily be removed by a predator (Darveau et al. 1997). Quail eggs averaged 26.6 mm in length and 20.4 mm in width, smaller than the more commonly used Japanese Quail eggs, and most closely resembling those of Swainson's Thrush (see Appendix A for scientific names of species found in study area), a common bird within the study area (Chapter 2).

In both 1998 and 1999, 720 nests (30 per stand) were exposed to possible predation for 12 days between June 2 and July 7, coinciding with the egg-laying and incubation period for most songbirds in the study area. In each stand, 15 point locations were randomly selected, using a grid with 20 by 20 m spacing and a random number table. The grid was centered on the point count station center, and rotated such that all grid points were at least 75 m from the edge of the stand to avoid potential edge effects on nest predation (see Paton 1994). At each point, one nest was placed on the ground and one in a shrub or small tree (0.5 - 2.0 m above ground) at random distances (< 10 m) and directions from the point. Nest location was constrained such that no nest was closer than 20 m to another nest of the same type. Nests were placed to approximate the nest location of actual songbirds, with ground nests most similar to those of the Dark-eyed Junco and shrub nests most similar to those of the Chipping Sparrow. Nests were checked six days after placement, and were re-checked and picked up six days later. The 12 day exposure period is similar to the incubation time for many ground- and shrub-nesting songbirds in the study area (Campbell et al. 2001). To reduce human scent, nests were aired for one week prior to use and disposable latex gloves were used when handling and checking nests. Predation was assumed when at least one of the eggs was bitten, pecked, eaten, or removed. Eggs remaining in the nests were collected and taken back to the field camp, where the marks on plasticine eggs were measured and compared to marks made by known predators (see *Predator Identification*). Quail eggs were inspected with a magnifying glass for scratches.

In 1999 concealment of each artificial nest was measured. A 6 x 12 cm board painted with 10 black and white checkered squares was held up to the nest at nest height and the number of squares covered at least 50 % by vegetation from a distance of 1 m at each of the four cardinal directions and above the nest was recorded. In addition, the distance from the nest to the nearest residual tree and to the nearest forest patch > 100 ha was estimated.

Predator identification

Two different approaches were used to build a library of marks made by known predators and to gain information on potential nest predator behavior. First, electronic cameras were used to obtain pictures of predators taking or marking the eggs. Cameras (Halina Prestige 280 AS or Pentax PC-33, both auto-advance and auto-focus) were attached to a TrailTimer® system, which was connected to a grass nest and an electronic treadle, on which a quail egg was placed. When an egg was disturbed, a picture was taken automatically. Cameras were placed on the ground in locations where potential nest predators had been sighted (not in experimental stands), and covered with black plastic and vegetation to conceal them and protect them from dew and rain. Six camera set-ups were placed out in 1998 for a total of 77 camera days.

Second, I observed the behavior of potential nest predators around artificial nests and eggs. Nests containing one quail and one plasticine egg were placed in areas frequented by red squirrels, ground squirrels, chipmunks, and Gray Jays, and their behavior around the nest was observed. Trials were conducted until at least three predation events from three different individuals from each species had been observed. Attempts to observe potentially important nocturnal predators (deer mice or red-backed voles) were not successful. Thus, three deer mice and three red-backed voles were caught in live traps, and transferred to individual holding cages (1 x 0.5 x 0.5 m) containing natural vegetation, water, and an artificial nest containing a quail egg and a plasticine egg. Their behavior was observed until they handled the eggs, or for no longer than 2 hours, after which they were released where they had been captured. Marks made on the eggs by each species were measured and described.

Based on these results, predators were grouped into three classes: small mammals (mice and chipmunks), squirrels (red and ground squirrels), and birds. Nests in which the quail egg was gone and the plasticine egg was untouched were classified separately. Given the results of the behavioral trials, these were likely squirrel or bird predation. If incisor markings > 5 mm wide were found on the plasticine egg, it was classified as 'other mammal'. These may have been snowshoe hare (*Lepus americanus*) or marten (*Martes americana*) (Darveau et al. 1997). If a quail egg was scratched and the plasticine egg was gone, or if both eggs were gone, the event was classified as unknown. Nests in which the quail egg was scratched but the plasticine egg was not marked were not considered depredated.

Analysis of Artificial Nest Data

I used general linear models to determine the influences of disturbance type, nest type, year, and residual tree density on the odds of predation, treating residual tree density as a covariate. Nests were grouped within replicate sites and thus were unlikely to be biologically or statistically independent. Due to the split plot nature of the experimental design (disturbance type and residual tree density were whole plot factors, nest type and year were split plot factors), I modeled the odds of predation as normally distributed, following a logit transformation, rather than as a binomial with potential overdispersion (M. Huso, Oregon State University, pers. comm.). The four main factors (disturbance type, residual tree density, nest type, year), all 2-way interactions, and one 3-way interaction (disturbance type* nest type* year) were included in the model, as these were variables of interest and interactions that were biologically most likely to occur. Four different models were run, with the dependent variables being the natural log odds of predation from all predators, from small mammals only, from squirrels only, and from birds only.

I used logistic regression to test the hypothesis that nest level variables (concealment, distance to nearest residual tree and forest patch) influenced probability of predation. To account for lack of independence among nests within a stand, each stand was assigned a number and this variable (standID) was forced into each model. All variables were entered into each model, along with nest type and interactions of each variable with nest type. Variable significance was assessed using the drop-in-deviance test. As with stand level models, four models were run to cover the three classes of predators and all predators combined.

Natural Nest Study

I monitored nests of open-cup ground and shrub nesting birds in four additional stands in 1998 and 1999. These stands were selected using the same criteria as for artificial nest stands, except that each had to be within a 15 minute drive from the field camp in order to facilitate nest searching and monitoring. I attempted to include burned stands in the natural nest study, but the lower abundance of birds in these stands, the difficulty of finding nests, and the distance of these stands from the field camp precluded this option.

Based on a preliminary study in 1997, nest searching efforts were focused on six species that nest in open-cups on the ground, in shrubs, or in low trees, that were abundant in the selected stands and whose nests were relatively easy to find: Dark-eyed Junco, Dusky Flycatcher, White-crowned Sparrow, Warbling Vireo, Wilson's Warbler, and Chipping Sparrow. Nests were located using systematic searches and by following birds carrying nesting material or food (Martin and Guelpel 1993). Once a nest was located, it was checked every 2-4 days until the young fledged or the nest failed. The number of eggs or chicks was recorded at each visit. Observations of nestlings within two days of expected fledging, fledglings near the nest, or parents feeding new fledglings within 25 m of the nest were considered to be indications of nest success (Martin 1993a). Predation was assumed when the contents of the nest disappeared more than two days before the expected fledging date. Nest predation was measured as the daily survival rate of nests (Mayfield 1975). Nests with uncertain fate were included in the calculation, and exposure days were terminated with the last observed active date for nests with uncertain fate and with the mid-point between the last observed active and the first observed inactive dates for nests of known fate (Manolis et al. 2000). The daily survival rate was calculated based on 26 days, which was the sum of the average incubation (12.3 days) and fledgling (12.3 days) times for the six focal species (based on Ehrlich et al. 1988) plus an extra day for incubation starting with the penultimate egg.

After each nest had succeeded or failed, nest concealment was measured as described above for artificial nests. Nest materials, height of nest rim above the ground, species and height of the supporting vegetation, and distance of the nest from the edge of the covering vegetation were also recorded. The number of shrub stems or tree branches and percent ground cover of ground, moss, grass, herbs, and down woody material within a 1-m radius plot centered on the nest were recorded. The percent cover of all shrubs with > 5 % cover was estimated within a 5-m plot centered on the nest. Four 10-m transects starting from the nest were established in each cardinal direction and all intersecting pieces of down woody material tallied and their diameter were recorded. Finally, all residual trees and snags were tallied by species and diameter class (3-11, 11-19, 19-27, 27-35, > 35 cm dbh) within a 20-m radius plot centered on the nest. The distance to the nearest residual tree and residual tree patch was measured, and the distance to the nearest forest patch > 100 ha was estimated.

Analysis of Natural Nest Data

I used multiple linear regression to determine if relationships existed between predation rate, density of residual trees in the stand, and year. F-tests or Mann-Whitney U-tests were used to test the hypothesis that depredated nests were closer to residual trees, residual tree patches, forest patches, or if they had a higher density of residual conifer trees within a 20 m radius of the nest than successful nests. Factors influencing predation on ground nests may differ from those on shrub nests, so nest types were analyzed separately. The small number of nests in each category precluded data analysis via logistic regression model building.

In addition to these hypothesis tests, I determined which nest vegetation variables differed between depredated and successful nests using F-tests or Mann-Whitney U-tests. Twenty-four variables were obtained from the measurements of concealment and vegetation around the natural nests. This number was reduced to eight by examining Pearson correlations among all variable pairs and dropping one variable from any pair with $r > 0.30$ and $p < 0.05$.

Predator Counts

To obtain an index of small mammal abundance, live-trapping was conducted in nine artificial nest stands and the four natural nest stands. In each stand, 94-96 Tincat® multiple capture traps were placed out on a 8 x 12 grid with trap stations spaced 15 m apart. Traps were locked open and pre-baited with apples and peanut butter for two nights then set for three nights and two days. Traps were checked each day from 05:30-10:00 h and from 18:00–21:00 h. Traps were covered with vegetation or logs to keep them cool during the day. All trapping was conducted from 8 July – 3 August 1999. Each captured animal was marked with an individually numbered ear tag in one ear, weighed, and its species, sex, and reproductive condition recorded. The number of captures per 100 trap-sessions was determined for total mammals, deer mice, red-backed voles, and chipmunks. When calculating the number of trap-sessions, a correction factor of half a trap-session was subtracted for each trap that was closed without having caught anything, or for traps that captured a previously tagged animal (Nelson and Clark 1973). The number of trap sessions used in these calculations varied by species, depending on the behavior of that species. Deer mice, which were only caught in the morning after a night of trapping, were considered exposed for three sessions; chipmunks, which are diurnal and only caught in the evening, for two sessions, and red-backed voles, which were caught both morning and evening, were considered exposed for five sessions.

Red squirrels and Gray Jays were counted in all stands using point counts. Each year, between 05:30 and 09:30 h from late May through early July, three 12-minute visits were made to the point count station near the center of each stand, and all red squirrels and Gray Jays visually or aurally detected within 150 m of the point count station recorded (see chapter 2 for details). To obtain an index of potential predators such as ground squirrels and chipmunks that are not well surveyed with point counts or small mammal trapping, the number of individuals of these species that was seen or heard while working in the stands was recorded, together with the total number of person-hours spent in that stand. The number of detections per person-hour was then calculated for each species.

Analysis of Predator Data

Indices of predator numbers were based on relatively few data. Thus, rather than allowing these variables to enter the models as predictive variables, I determined if the patterns in predator numbers were similar to patterns of nest predation by those predators. Specifically, for each species, I used general linear models to determine 1) the relationship between the index of abundance of predators in the artificial nests stands and the residual tree density and disturbance type of those stands, and 2) the relationship between the index of abundance of that predator and the odds of predation by that predator on artificial nests (logit transformed). Where there were too few detections or incidences of predation to use this approach, I used Chi-square analysis to determine if the presence of the species was related to the presence of predation by the that class of predators.

Songbird Abundance

Songbirds were surveyed in each of the 28 stands each year using point counts, following the methods outlined for red squirrels. The mean abundance of all songbird species and of only ground- and shrub/low tree-nesting species was calculated for each year using adjustments for detectability, following methods outlined in Chapter 2. Relationships between odds of predation on artificial nests and mean abundance of ground and shrub nesting songbirds were analyzed with a simple linear regression for each year separately, following a logit transformation on the odds of predation. Relationships between predation rate on natural nests and mean abundance of ground- and shrub-nesting songbirds were analyzed with a simple linear regression for each year separately.

SAS version 6.12 (SAS 1996) was used for all analyses. Variables were assessed by residual plots and box-plots of the residuals and transformed as necessary to meet the assumptions for logistic and multiple linear regression. A P value of 0.10 was considered significant because of the relative ramifications of making Type II errors in applied research (Steidl et al. 1997).

Results

Identification of Nest Predators

Six species of nest predators were identified from photos taken using remote cameras. Photos were obtained of six red squirrels, three golden-mantled ground squirrels, one Columbia ground squirrel, six deer mice, one yellow pine chipmunk, and three Gray Jays removing or handling eggs. Each species was also observed taking or eating eggs from the artificial nests during the behavioral trials. Deer mice attempted to bite through the apex end of the quail eggs, but were not successful in any trials. They succeeded in rolling the egg out of the nest in two of nine trials, and their handling of the egg left definitive scratch marks on it. Each individual bit a plasticine egg at least once. Red-backed voles ignored the nest and both eggs in each trial. Red squirrels and Gray Jays were observed removing the natural egg from the nest, but in most cases left the plasticine egg untouched. Red squirrels and ground squirrels sometimes ate the quail egg in the nest, leaving large fragments; they were the only predators observed to do this. Chipmunks were also able to remove the quail egg from the nest by rolling it out, but were not observed breaking the egg. Measurements of the teeth marks left in the plasticine eggs by these predators revealed that deer mice left marks 1 – 1.5 mm wide, chipmunks 1 – 2 mm wide, red squirrels 3 mm wide, and ground squirrels 3-4 mm wide. Jays generally left deep, triangular beak marks 3-6 mm wide, but in one case left a smaller triangular mark 1.5 mm wide.

Artificial Nests

Predation on artificial nests was higher in 1998 than in 1999 (Table 3.1). In 1998, the majority of nest predators were small mammals, followed by unknown predators, birds, and instances in which only the quail egg was removed from the nest (likely birds or squirrels). Most of the difference between years was accounted for by the difference in the amount of predation by small mammals. In 1999, predation from small mammals was nearly three times lower than in 1998, and was similar to that from unknown predators. The percentages of nests preyed on by squirrels, birds, and unknown predators was similar in both years. Predation from other mammals was very low in both years (Table 3.1).

The odds of predation on artificial nests was significantly influenced by density of residual trees, but only for logged stands in 1998 (Table 3.2). Year was a significant factor, with predation higher in 1998 than in 1999, and there were significant interactions between residual tree density and disturbance type, between residual tree density and year, and between disturbance type and nest type (Table 3.2). In 1998, a five-fold increase in the density of residual trees led to a doubling of the odds of predation on artificial nests in logged stands but there was no influence of residual tree density on predation in burned stands (Table 3.2, Figure 3.2). In 1999 there was no significant influence of residual tree density on nest predation in either burned or logged stands; residual tree density had to be increased over 100 times to double the odds of predation in logged stands, while the negative effect size for burned stands indicates that increasing residual tree density 100 fold actually led to a halving of predation in burned stands (Table 3.2, Figure 3.2).

Table 3.1 Percentage of artificial nests preyed upon by the various predator classes for each nest type-disturbance type combination, each year. G - ground nests, S – shrub nests. Percentage calculations were based on the total number of nests recovered. A total of 120 nests of each type were placed out in burned stands (n=8) and 240 of each type in logged stands (n=16).

		Nest Type	**Small Mammal**	**Squirrel**	**Bird**	**Quail Egg Gone**	**Other Mammal**	**Unknown**	**Total Predated**	**# Nests recovered**
1998	Burned	G	48.6	3.5	5.3	2.6	0.9	7.1	68.3	113
		S	33.0	0	1.7	16.1	0.9	2.7	54.4	112
	Logged	G	36.6	3.9	4.7	6.5	0	7.7	59.4	232
		S	19.1	4.7	14.8	9.3	0	17.4	65.3	236
		Overall	**32.0**	**3.5**	**7.8**	**8.4**	**0.3**	**10.1**	**62.2**	**693**
1999	Burned	G	19.7	0.9	3.4	4.3	0	9.4	37.7	117
		S	7.9	1.8	6.1	5.2	2.6	11.4	35.0	114
	Logged	G	15.5	8.2	4.7	1.7	0	5.6	35.7	232
		S	7.7	5.1	12.0	1.7	0.4	15.0	41.9	234
		Overall	**12.3**	**4.9**	**7.2**	**2.7**	**0.6**	**10.3**	**38.0**	**697**

Table 3.2 Results of the general linear model analysis on the influence of residual trees, disturbance type, nest type and year on the odds of predation by predator type Significance differences ($p < 0.10$) shown in bold. For all models, $n=96$, $p < 0.001$. ResTree – residual tree density, Disturbance –burned or logged, Year – 1998 or 1999, Type - ground or shrub, ndf = numerator degrees of freedom, ddf = denominator degrees of freedom. Effects are interpreted as an x-(effect size) fold increase in the density of residual trees led to a doubling of the odds of predation on artificial nests. Effects greater than 100 indicate no measurable effect of residual trees on the odds of predation and are shown only as > 100, and 95 % Confidence Intervals (CI) not calculated was not calculated for these.

			All predators		**Small Mammals**		**Squirrels**		**Birds**	
Model Terms	**ndf**	**ddf**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Disturbance	1	20	1.86	0.189	2.00	0.173	0.54	0.469	1.33	0.262
Residual Trees	1	20	1.71	0.206	2.76	0.112	1.40	0.251	**3.61**	**0.072**
ResTree*Disturbance	1	20	**3.56**	**0.074**	1.31	0.266	**3.60**	**0.072**	**5.99**	**0.024**
Nest Type	1	64	0.05	0.831	1.60	0.211	0.66	0.421	0.89	0.350
Disturbance*Type	1	64	**4.83**	**0.032**	0.53	0.467	1.82	0.183	**9.41**	**0.003**
ResTree*Type	1	64	0.18	0.671	0.94	0.336	0.24	0.627	0.00	0.971
Year	1	64	**3.72**	**0.058**	**11.72**	**0.001**	0.59	0.444	0.26	0.610
Disturbance*Year	1	64	0.04	0.848	0.68	0.412	0.39	0.533	0.04	0.845
ResTree*Year	1	64	**9.22**	**0.004**	**7.19**	**0.009**	**3.99**	**0.050**	**8.36**	**0.005**
Type*Year	1	64	0.39	0.536	0.29	0.589	1.15	0.288	**2.89**	**0.094**
Disturbance*Type*Year	1	64	0.39	0.536	0.07	0.790	**3.97**	**0.051**	**4.59**	**0.036**

Effect of Residual Trees on predation	**Effect**	**95 % CI**	**Effect**	**95 % CI**	**Effect**	**95 % CI**	**Effect**	**95 % CI**
1998 – Logged	5.13	2.65, 151.5	9.97	2.94, 200.6	10.12	3.93, 179.3	5.63	3.11, 37.2
1998 – Burned	> 1000		> 100		> 1000		> 1000	
1999 - Logged	> 100		> 1000		> 100		51.3	
1999 – Burned	-96		- 999		- 998		-99	

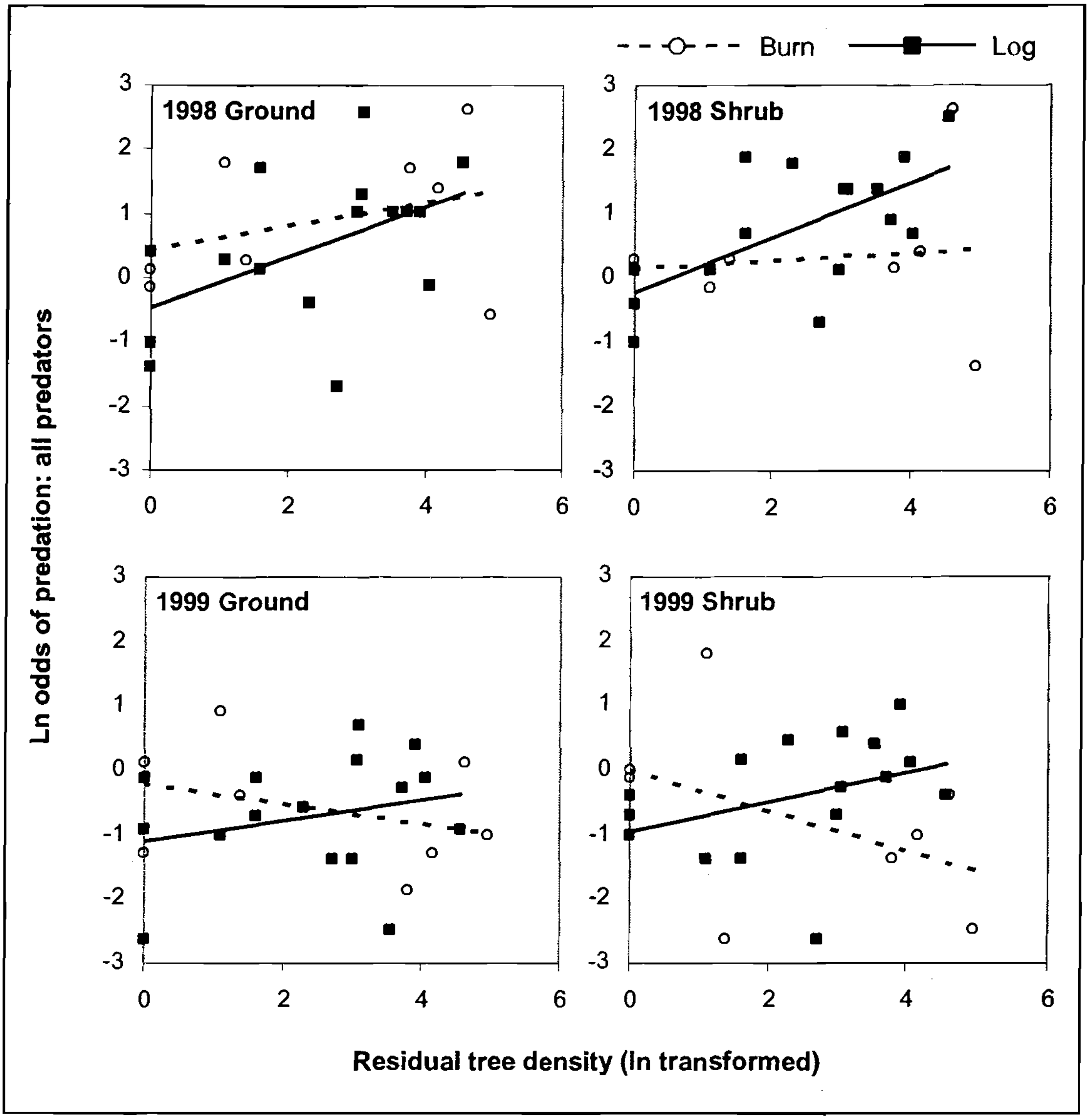


Figure 3.2 Linear relationships between the density of residual trees, and the natural log (ln) odds of predation by all predators, for each of the nest types in each year.

The interaction between disturbance type and nest type is reflected in a slight increase in predation with residual trees in logged stands, but no effect or a slight decrease in predation on nests in burned stands. There was high variability among stands in each disturbance type (Figure 3.2).

When predation by small mammals was modeled, there was a large difference in predation between years, and a significant interaction between residual trees and year (Table 3.2). The odds of predation were higher in 1998 than in 1999 (Table 3.2), and there was a significant effect of residual tree density of predation in logged stands in 1998. In 1998, increasing the density of residual trees 10-fold produced a doubling of the odds of predation on artificial nests in logged stands (Table 3.2, Figure 3.3).

In the model of predation by squirrels, interactions between residual tree density and disturbance type and between residual tree density and year were significant (Table 3.2), reflecting the fact that increasing the density of residual trees by 10-fold was required to produce a doubling of the odds of predation in logged stands in 1998 (Table 3.2, Figure 3.4). There was also a 3-way interaction between year, disturbance type and nest type, reflecting a slight increase in predation with residual tree density in logged stands and a decrease in burned stands in 1999 only (Figure 3.4).

The model of predation by birds was the only one in which the residual tree variable was significant in addition to significant interactions between residual tree density and disturbance type, between residual tree density and year, between disturbance type and nest type, and between nest type and year (Table 3.2, Figure 3.5). These are reflected by the 5.6 fold increase in residual tree density needed to produce a doubling of the odds of predation in logged stands in 1998, and a 51.3 fold increase needed to produce the same effect in 1999 (Table 3.2). As with the other models, the effect of residual tree density in burned stands was either neutral or had opposite effect to that in logged stands (Figure 3.5).

Because events in which the quail egg was gone and the plasticine egg was unmarked were likely squirrels or jays, for analytical purposes these cases were first, assumed to be all due to birds and second, assumed to be all due to squirrels. In neither instance did the significant variables in the models change.

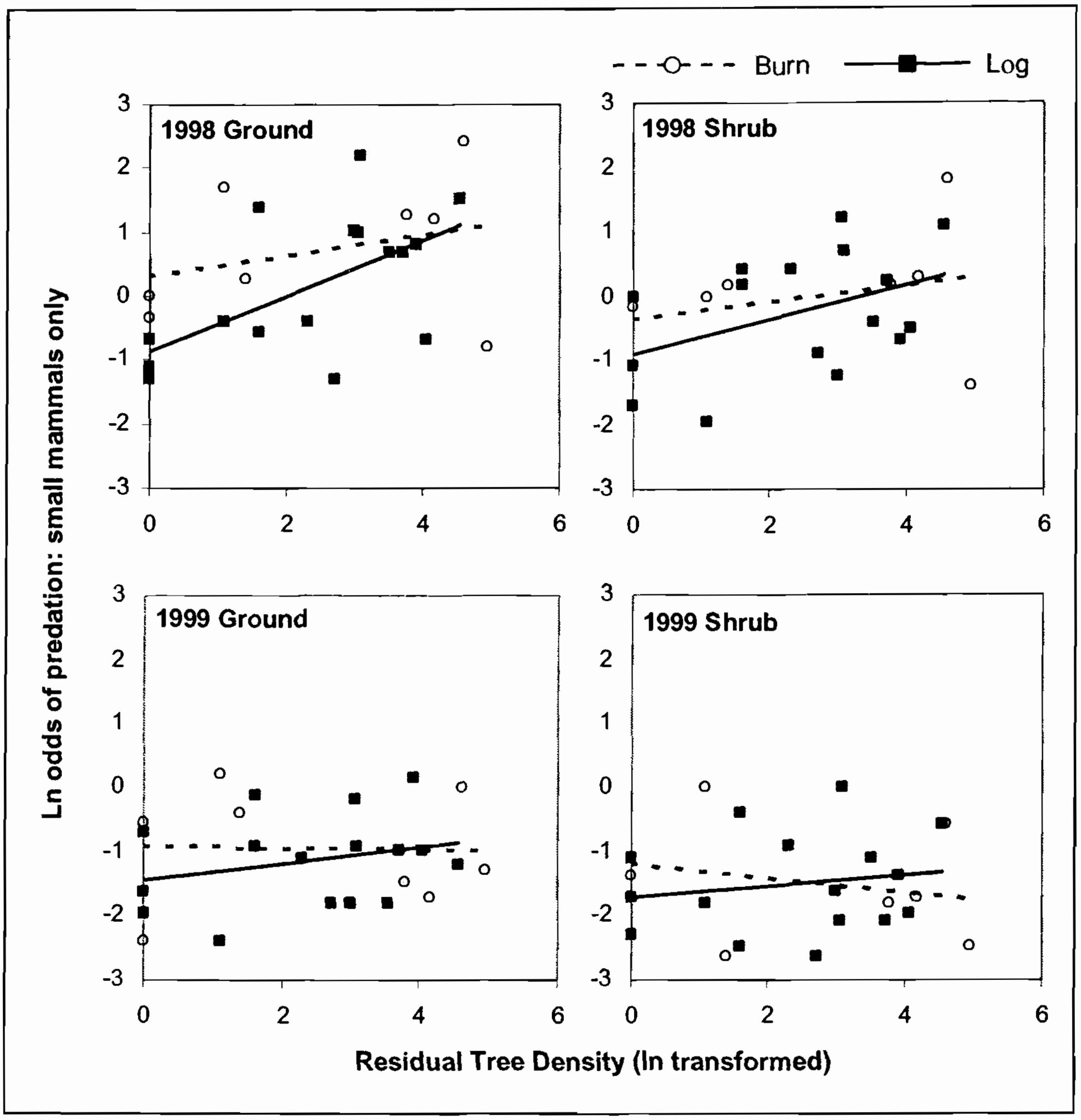


Figure 3.3 Linear relationships between the density of residual trees and the natural log (ln) odds of predation by small mammal predators, for each nest-type year combination.

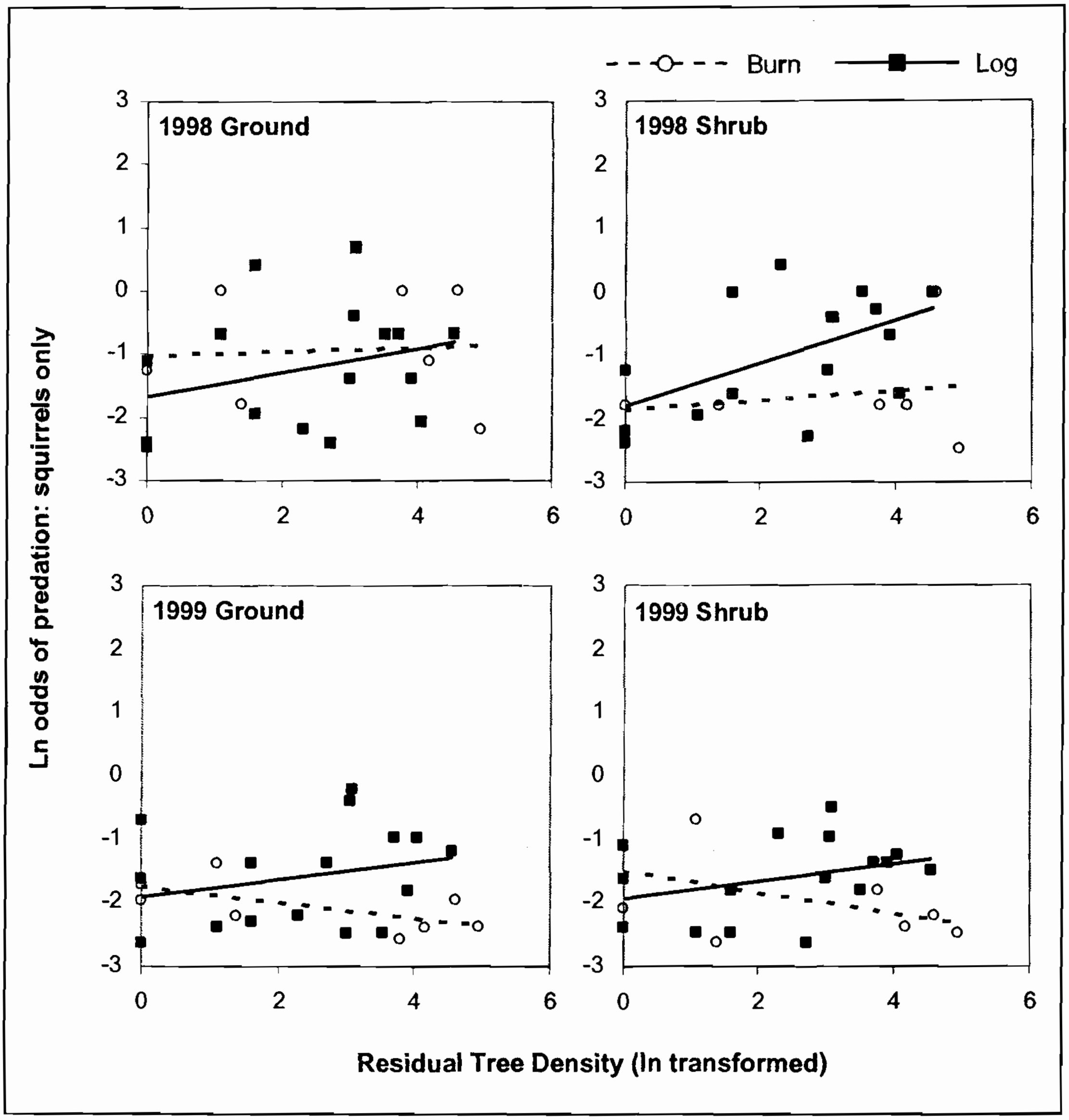


Figure 3.4 Linear relationships between the density of residual trees and the natural log (ln) odds of predation by squirrels, for each nest-type year combination.

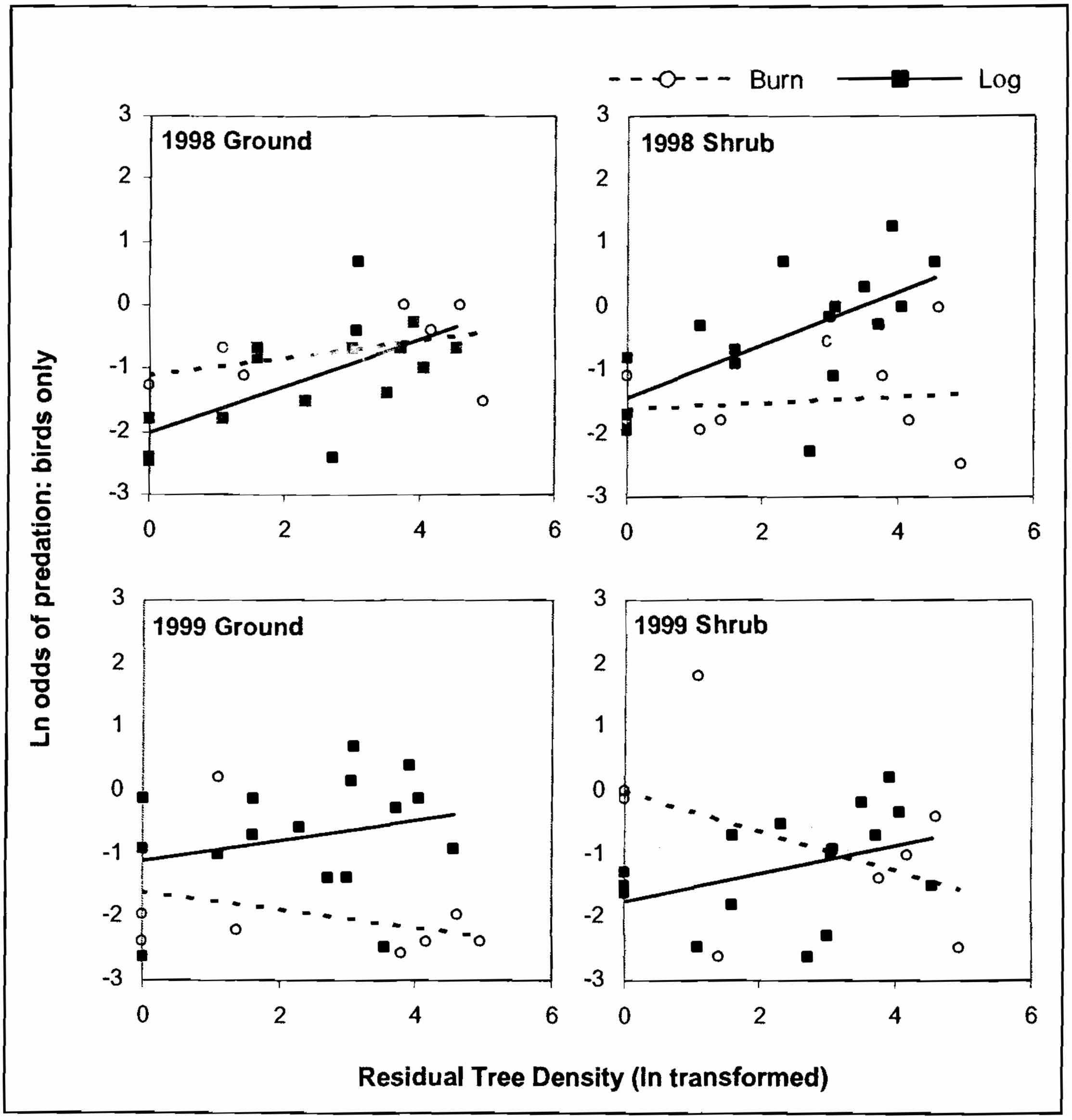


Figure 3.5 Linear relationships between the density of residual trees and the natural log (ln) odds of predation by birds, for each nest-type year combination.

Depredated ground and shrub nests had statistically lower concealment than successful nests (Table 3.3), although the difference was very small (Table 3.4). Nests depredated by small mammals had statistically lower concealment than successful nests (Table 3.4), although again this difference was very small. Small mammals depredated more ground nests than shrub nests (Table 3.3). In both these models the stand identification variable was highly significant (Table 3.3), indicating high variability among stands. The models for birds and squirrels were poor and would not converge due to the small number of predations by these species. Thus, the StandID variable was removed, and the p value considered significant reduced from 0.10 to 0.05. Results from these models must be interpreted with caution. When this was done, nests depredated by birds were closer to residual trees than were successful nests (Table 3.3, 3.4). No variables were statistically significant in the model for squirrel predation. Although distance to the nearest residual tree was not significant in any model, there were trends for depredated nests to be closer to residual trees than successful nests, for all predators, particularly birds and squirrels (Table 3.4). Distance to the nearest large forest patch was not significant in any model.

Table 3.3 Results of logistic regression analysis on the effects of nest concealment, nest type, residual tree density within a 20 m radius of the nest, and distance to the nearest large forest patch, on the probability of predation on artificial nests, by predator type. Terms not shown were not statistically significant (p >0.10).

	Significant terms	χ^2	**p**
All predators	Stand ID	108.2	0.0001
	Concealment	6.08	0.014
Small Mammals	Stand ID	46.12	0.0008
	Nest Type	10.17	0.001
	Concealment	3.09	0.08
Birds	Residual Trees	3.84	0.05
Squirrels	none		

Table 3.4 Mean percentage of concealment (± SE), distance to the nearest residual tree, and distance to the nearest large forest patch (in categories) for successful and predated artificial nests, by predator class.

		Successful	**Predated by:**			
			All Predators	**Small Mammals**	**Birds**	**Squirrels**
Concealment (%)	Ground	82.8 ± 1.3	80.6 ± 1.7	79.0 ± 2.8	88.2 ± 3.6	82.5 ± 4.2
	Shrub	48.5 ± 2.0	43.2 ± 2.2	46.1 ± 3.6	39.5 ± 4.4	52.1 ± 7.4
Distance to nearest Residual Tree (m)	Ground	48.4 ± 5.6	47.9 ± 7.4	42.7 ± 9.9	25.4 ± 7.8	25.8 ± 14.7
	Shrub	52.1 ± 5.9	40.8 ± 6.2	34.1 ± 12.9	18.0 ± 3.7	15.7 ± 4.0
Distance to nearest forest patch*	Ground	3.48 ± 0.10	3.61 ± 0.13	3.65 ± 0.20	3.47 ± 0.39	3.13 ± 0.35
	Shrub	3.50 ± 0.10	3.48 ± 0.13	3.62 ± 0.28	3.44 ± 0.25	3.29 ± 0.41
Sample size	Ground	202	117	51	15	16
	Shrub	192	128	21	33	14

* distance to nearest forest patch divided into five categories, 1 = < 50 m, 2 = 51 – 100 m, 3 = 100 – 300, 4 = 300 – 500 m, 5 > 500 m

Natural Nests

A total of 72 natural nests were found in the four searched stands in 1998 and 1999 (Table 3.5). Eighty one percent of these were of the six focal species; Dark-eyed Junco (16 nests), White-crowned Sparrow (12), Dusky Flycatcher (10), Warbling Vireo (9), Chipping Sparrow (6), and Wilson's Warbler (5). Other species included Townsend's Solitaire (3 nests), Hermit Thrush (3), American Robin (2), Lincoln's Sparrow (2), Olive-sided Flycatcher (1), Pine Grosbeak (1), Yellow-rumped Warbler (1) and Cassin's Finch (1). No nests were parasitized by the Brown-headed Cowbird. Ground nests were placed predominantly in pine grass (76%), followed by Labrador tea (*Ledum groenlandicum,* 10%). Shrub and low tree nests occurred predominately in Sitka alder (31%), but were also found in saskatoon (*Amelanchier alnifolia*, 14%), willow (*Salix* sp. 9%), lodgepole pine (14%), subalpine fir (14%), Douglas-fir (11%), and Engelmann spruce (8%). There was no statistically significant difference in the success rate between ground and shrub nests in 1998 or 1999 (1998: $\chi^2 = 1.01$, df=2, p=0.60, 1999: $\chi^2=0.14$, df=2, p=0.93). Thus, nests of both types were combined for analysis.

In 1998 nest success among the four stands ranged from 0.51 to 0.71 (Table 3.5). Few nests failed due to exposure (n=3, 9 %) or predation (n=4, 12 %). The predation rate varied among stands from 0.20 to 0.32, with a mean of 0.26 (Table 3.5). In 1999, nest success was lower, ranging from 0.23 to 0.63, due to increased losses from both exposure (n=9, 23 %) and predation (n=9, 23 %). The predation rate varied from 0.21 to 0.53, with a mean of 0.42 (Table 3.5). There was no significant relationship between the predation rate and the density of residual trees in either year, nor was there a difference in predation rate between years (F = 1.15, df = 7, p=0.43; Figure 3.6). Although there was a trend for nest success to increase with the density of residual trees (Figure 3.6), this was not significant in either year (F=1.83, df=7, p=0.28). However, if years were examined separately, there was a significant relationship between nest success and residual tree density in 1998 (1998: F=9.86, df=3, p=0.09; 1999: F=0.16, df=3, p=0.72).

None of the residual tree variables differed between depredated and successful nests, for either shrub or ground nests (Table 3.6). Residual conifer density surrounding the nest, distance to the nearest residual tree, distance to the nearest residual patch, and distance to the nearest large forest patch were all similar between depredated and successful nests (Table 3.6).

Table 3.5 The number of real nests found in each stand and their fate, by year. Percentages are shown in parentheses. Predation rate = 1 – Survival Rate, excluding nests that failed due to exposure or abandonment.

Year	Stand - Density of Residual Trees	n	Successful	Exposure/ Abandoned[1]	Predated	Unkn. Fate	Exposure days (total)[2]	Nest Success (26 days)	Exposure days (no exp/aban)[3]	Predation rate (26 days)
1998	64/ha	5	4	0	1 (20)	0	77	0.71	77	0.29
	32/ha	7	6	0	1 (14)	0	69	0.68	69	0.32
	8/ha	10	7	1 (10)	1 (10)	1	116.5	0.51	97.5	0.24
	14/ha	11	8	2 (18)	1 (9)	0	130.5	0.55	117	0.20
	TOTAL/ MEAN	**33**	**25**	**3 (9)**	**4 (12)**	**1**	**393**	**0.61**	**360.5**	**0.26**
1999	64/ha	14	6	3 (21)	4 (29)	1	201.5	0.40	141	0.53
	32/ha	7	4	1 (14)	1 (14)	1	114.5	0.63	110	0.21
	8/ha	8	4	2 (25)	2 (25)	0	112	0.39	79	0.49
	14/ha	10	5	3 (30)	2 (20)	0	91	0.23	84.5	0.46
	TOTAL/ MEAN	**39**	**19**	**9 (23)**	**9 (23)**	**2**	**519**	**0.41**	**414.5**	**0.42**

[1] number of nests that failed due to exposure or abandonment.

[2] total number of days for all nests.

[3] total number of days for nests, excluding those that failed due to exposure or abandonment.

Table 3.6 Residual tree and vegetation variables with their means and standard errors for predated and successful natural nests. Variables compared with ANOVA, those compared with Mann-Whitney U-tests indicated with a † .

	Ground Nests				Shrub Nests			
	Predated (n=7)	**Successful** (n=24)	F or χ^2	p	**Predated** (n=8)	**Successful** (n=20)	F or χ^2	p
Residual conifer density (# / 0.13 ha) †	2.9 ± 1.1	4.1 ± 0.9	0.51	0.47	4.5 ± 1.9	5.9 ± 1.2	1.05	0.31
Distance to nearest residual tree (m)	19.1 ± 5.8	15.5 ± 3.0	0.52	0.47	18.7 ± 5.6	10.6 ± 3.4	2.30	0.14
Distance to nearest residual patch (m)	37.3 ± 14.6	38.5 ± 12.3	0.32	0.57	51.8 ± 15.4	48.8 ± 16.5	1.22	0.27
Distance to nearest large forest patch (> 100 ha) [1] †	3.8 ± 0.3	3.4 ± 0.2	0.16	0.69	3.7 ± 0.4	3.6 ± 0.2	1.38	0.24
Nest concealment (%)	89.7 ± 2.9	87.3 ± 2.6	0.01	0.93	55.2 ± 5.9	73.9 ± 3.8	12.23	0.001
Nest height off ground (m)	-	-	-	-	1.08 ± 0.20	1.45 ± 0.15	1.62	0.20
Distance from edge of nest to outer edge of nest tree/shrub (cm) †	-	-	-	-	0.32 ± 0.12	0.50 ± 0.08	2.06	0.15
Grass Cover (%)	65.0 ± 11.0	56.0 ± 6.7	0.51	0.48	43.3 ± 11.6	37.6 ± 6.0	0.08	0.78
Low Shrub (< 2 m) Cover (%)†	19.0 ± 10.2	14.3 ± 3.4	0.06	0.98	14.8 ± 5.0	11.2 ± 4.0	1.41	0.23
Tall Shrub Cover (%)†	0.0 ± 0.0	4.2 ± 3.7	-	-	22.5 ± 12.0	34.8 ± 8.6	1.27	0.25
CWD Volume (m3/ha)	172 ± 48	126 ± 14	0.43	0.52	116 ± 20	176 ± 28	1.09	0.31
Density of regenerating conifer trees (# /.13 ha) †	67.0 ± 39.1	58.5 ± 14.4	0.005	0.94	71.5 ± 27.1	57.6 ± 17.3	0.04	0.84

[1] distance to nearest forest patch divided into five categories: 1 = < 50 m; 2 = 51 – 100 m; 3 = 100 – 300; 4 = 300 – 500 m; 5 > 500 m

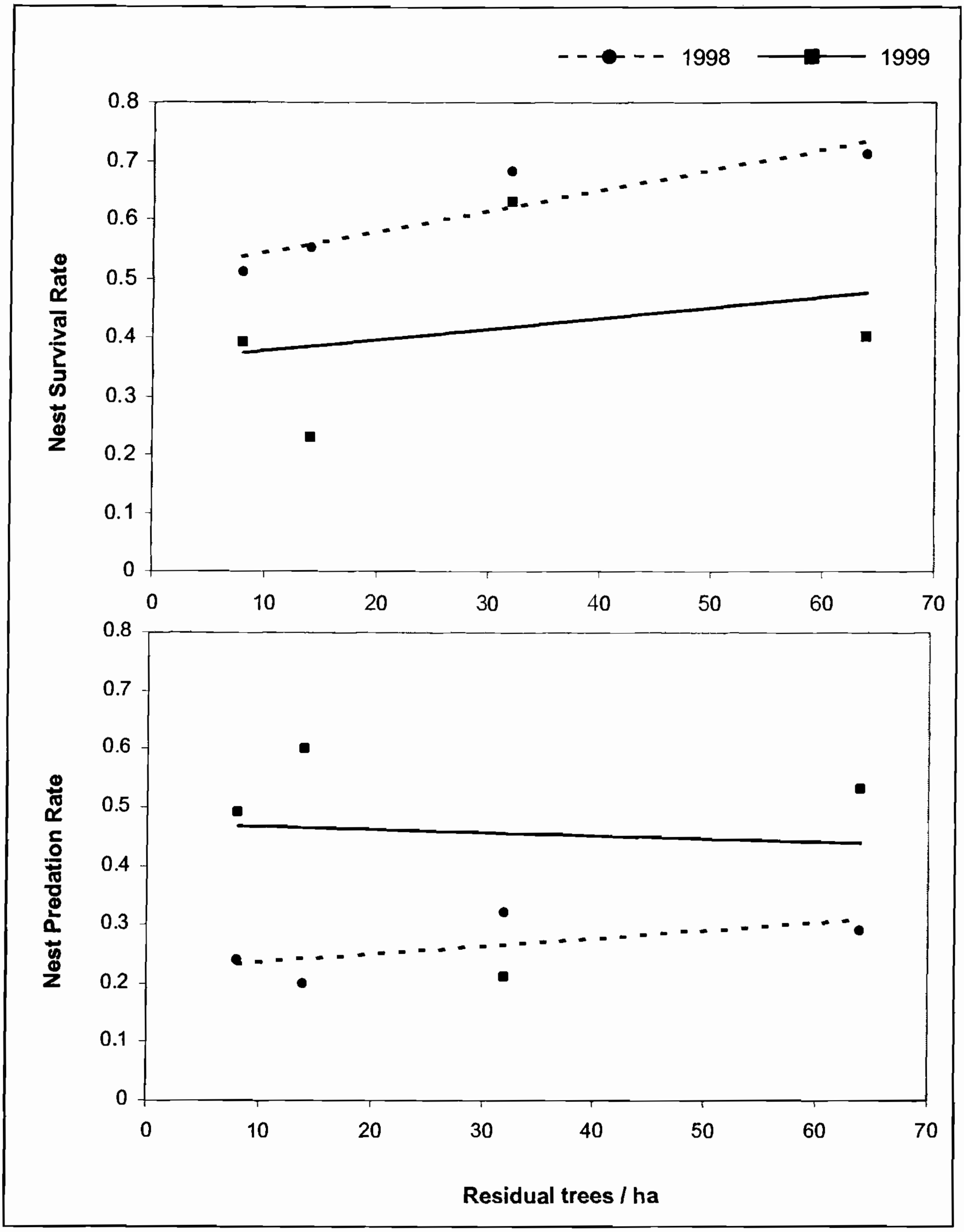


Figure 3.6 Linear trends in survival and predation rates for natural nests relative to residual tree density in 1998 and 1999.

Of the other set of vegetation variables, eliminating highly correlated variables left eight variables; concealment, nest height, distance from the edge of the nest to the outer edge of the vegetation, grass cover, low shrub cover, tall shrub cover, coarse woody debris volume, and density of regenerating conifer trees. Of these, only concealment differed between depredated and successful nests, and only for shrub nests (Table 3.6).

Predators within Artificial Nest Stands

The number of detections of red squirrels was greater in logged than burned stands ($\chi^2 = 6.51$, df=1, p=0.01), greater in 1998 than 1999 ($\chi^2 = 5.29$, df=1, p=0.02), and increased with residual tree density ($\chi^2 = 4.59$, df=1, p=0.03, Table 3.7, 3.8). There were no significant linear relationships between the number of detections of red squirrels and the odds of predation by squirrels in either year or for either nest type (1998 shrub; F=0.99, df=23, p=0.33, 1998 ground; F=0.043, df=23, p=0.84; 1999 ground F=1.36, df=23, p=0.26, 1999 shrub; F=0.33, df=23, p=0.57, Table 3.7).

The number of detections of ground squirrels was greater in logged than burned stands ($\chi^2 = 6.45$, df=1, p=0.01), but did not differ between years ($\chi^2 = 0.03$, df=1, p=0.85, Table 3.7), and decreased with residual tree density ($\chi^2 = 6.34$, df=1, p=0.01, Table 3.8). There was a significant relationship between the detection of ground squirrels and the odds of squirrel predation for ground nests in 1998 ($\chi^2 = 8.00$, df=1, p=0.005) but not in 1999 ($\chi^2 = 0.94$, df=1, p=0.76, Table 3.8). However there were no significant relationships when the abundance of ground and red squirrels was combined and modeled in relation to the odds of predation by squirrels on shrub and ground nests combined (1998 F=0.68, df=23, p=0.42, 1999 F=0.11, df=23, p=0.75)

Gray Jays were detected more often in logged stands than burned stands ($\chi^2 = 6.44$, df=1, p=0.01), but the number of detections of Gray Jays was not related to residual tree density ($\chi^2 = 0.80$, df=1, p=0.37), nor did it differ between years ($\chi^2 = 1.10$, df=1, p=0.30, Table 3.7, 3.8). The detection of Gray Jays and the presence of bird predation was significantly related for shrub nests in both years ($\chi^2 = 2.92$, df=1, p=0.09), but not for ground nests ($\chi^2 = 0.22$, df=1, p=0.88, Table 3.8). Although perch sites were plentiful in some of the stands, Gray Jays were rarely observed using them.

Table 3.7 The mean index of abundance ± SE of predators by disturbance type and year. The number of stands each predator species was detected at is in parentheses following the standard error. Data for red squirrels and gray jays from point counts, data for chipmunks and ground squirrels from person-hours of observations (1998, 140.7 observer-hours; 1999, 575.1 observer-hours).

	1998		**1999**	
	Burn (n=8)	**Log** (n=16)	**Burn** (n=8)	**Log** (n=16)
Red Squirrel	0.38 ± 0.25 (2)	0.65 ± 0.17 (10)	0.08 ± 0.05 (2)	0.29 ± 0.07 (9)
Gray Jay	0 ± 0 (0)	0.15 ± 0.07 (5)	0.04 ± 0.04 (1)	0.21 ± 0.7 (7)
Ground Squirrel	0.08 ± 0.06 (2)	0.23 ± 0.12 (5)	0 ± 0 (0)	0.19 ± 0.14 (7)
Chipmunk	0.13 ± 0.09 (4)	0.26 ± 0.10 (10)	0.05 ± 0.03 (3)	0.24 ± 0.06 (15)

Table 3.8 Qualitative summary of the relationship between the various indices of predator abundance and disturbance type, residual tree density, year, and the odds of predation on artificial nests by predators of that type.

Predator	**Disturbance Type**	**Residual Trees**	**Year**	**Positively related odds of predation**
Red squirrels	Greater in logged	Increased	higher in 1998	no
Ground squirrels	Greater in logged	decreased	no difference	yes, ground nests in 1998 only
Gray jays	Greater in logged	no response	no difference	yes, shrub nests only
Chipmunks	Greater in logged	no response	no difference	no
Deer mice	not examined	increased	not examined	yes
Red-backed voles	not examined	no response	not examined	no

Raptors were never observed using these perches, although red-tailed hawks and northern goshawks were observed doing so in other stands (unpubl. data). Common ravens were observed flying high over the stands, but rarely landing within them. American crows were never detected, and Steller's jay was detected only once in one logged stand.

Small mammal captures were comprised of red-backed voles (40% of total captures), deer mice (28%), chipmunks (17%), shrews (*Sorex* spp. 8%), mountain phenacomys (*Phenacomys intermedius* 5%), and western jumping mouse (*Zapus princeps*, 2%). Since traps were placed only in logged stands in 1999, no comparison between logged and burned stands or between years was possible. On average, in the nine artificial nests stands there were 1.28 ± 0.84 (SE) deer mice captures and 1.86 ± 0.93 red-backed voles captures per 100 trap sessions. The number of deer mouse captures was positively related to the number of residual trees (F=27.9, df=7, p=0.001, r^2=0.84), but the effect was very small, with an increase of one deer mouse capture per 100 trap-sessions for every increase of 67.6 residual trees per ha. The abundance of red-backed voles was not related to residual tree density (F=1.61, df=7, p=0.24). There was a strong linear relationship between the total number of small mammals captured per 100 sessions and the odds of predation by small mammals (F=37.8, df=8, p=0.0005, r^2 = 0.84). When species were examined individually, there was also a strong positive relationship between the odds of small mammal predation and the number of deer mice (F=47.82, df=8, p=0.0005) but not of red-backed voles (F=0.75, df=8, p=0.42) nor chipmunks (F=0.051, df=8, p=0.83, Table 3.8).

Results from observer data for chipmunks were similar to that from the trapping data in that there were no significant relationships between the detections of chipmunks and the odds of predation by small mammals in either year (1998 ground; F=1.24, p=0.28; 1998 shrub F=0.03, p=0.86; 1999 ground F=0.41, p=0.53; 1999 shrub F=0.95, p=0.34; df=23 for all models). The abundance of chipmunks was higher in logged than burned stands (F=26.2, df=1, p=0.001, Table 3.7), but did not vary with residual tree density (F=0.09, df=1, p=0.35), or year (F= 0.56, df=1, p = 0.46, Table 3.8).

To obtain an index of predator numbers, the indices of abundance for red and ground squirrels, Gray Jays, and chipmunks were added. There were no significant linear relationships between this index of predator abundance and the total odds of predation on ground and shrub nests in either year (1998: F=0.36, df=23, p=0.55; 1999: F=0.0008, df=23, p=0.97). However, when deer mice were added to this index there was a significant relationship between the index of predator abundance and predation on artificial nests for the nine stands in which small mammal trapping was conducted (F=44.47, df=8, p = 0.0006, r^2= 0.88, Figure 3.7). Adding red-backed voles to the index did not improve the regression significantly (F=44.98, df=8, p=0.0005, r^2=0.89).

Predators within Natural Nest Stands

Due to the fact that the point counts for jays and red squirrels in the natural nest stands detected no jays in any of the stands and only one red squirrel in one of the stands each year, observational data were used as an index of abundance for all predator species. Chipmunks were the most commonly seen predators in the natural nest stands, followed by red and ground squirrels (Table 3.9). Gray Jays were rarely observed. More red squirrels and chipmunks were detected per hour in 1998 vs. 1999 (Table 3.9). However, there were no clear patterns in the number of predators seen per observer hour and the predation rate. In 1998, red squirrels were strongly positively correlated with the predation rate, while ground squirrels and chipmunks were negatively correlated (Table 3.9). There were too few detections of Gray Jays for analysis. In 1999, red squirrels, chipmunks, mice and voles were negatively correlated with the predation rate, while ground squirrels were positively correlated. However, in this year one stand (with 32 residual trees/ha) had a much lower predation rate than the other stands (Table 3.9) and thus was highly influential in determining correlations. When this stand was removed from the correlation calculations, red squirrels, Gray Jays, deer mice and ground squirrels were positively correlated with the predation rate, while chipmunks were negatively correlated. When an index of predators was obtained by adding the indices of abundance for all species, there was a positive correlation between the total number of predators and the predation rate in 1998 (r = 0.91) but in 1999 the opposite was true (r = -0.97, Table 3.9, Figure 3.8). Adding deer mice and red-backed voles to the index in 1999 did not change the direction of the correlation (-0.94, Figure 3.8).

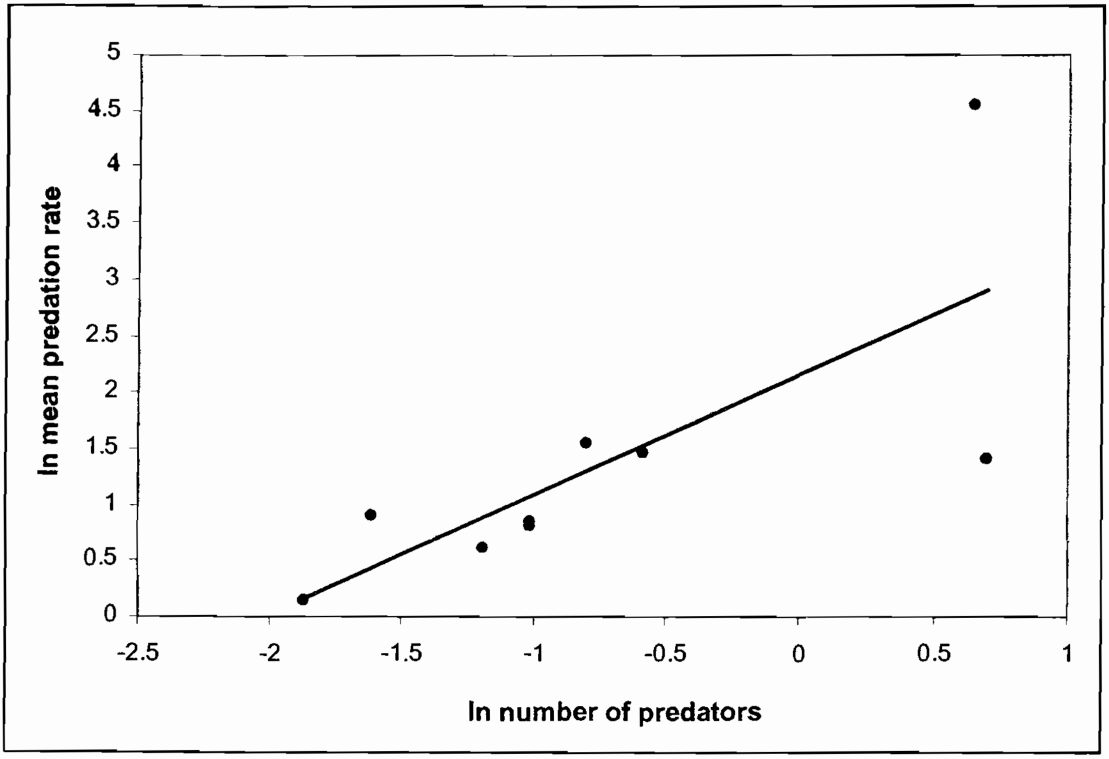


Figure 3.7 Relationship between the total number of predators (natural logged) and the total odds of predation (natural logged) on artificial shrub and ground nests combined, in 1999, for the nine stands in which small mammal trapping was conducted.

Table 3.9 The number of predators seen per hour in each of the natural nest stands, along with the total number of hours spent in those stands, by year. The correlation (r) between each species and the predation rate is shown underneath the total. For 1999, the number in parentheses is the correlation rate without the stand with 32 residual trees/ha. For deer mice and red-backed voles numbers are the number captured per 100 trap sessions. Trapping was conducted in 1999 only.

Year	# Residual Trees / ha	Total Hours	Gray Jay	Red Squirrel	Ground Squirrel	Chipmunk	Deer Mouse	Red-backed Vole	Total Predators (without small mammals)
1998	64	26.8	0.00	0.30	0.07	0.67	-	-	1.04
	32	41.8	0.10	0.43	0.14	0.46	-	-	1.13
	14	42.5	0.00	0.09	0.26	0.61	-	-	0.96
	8	40.0	0.00	0.15	0.23	0.60	-	-	0.98
	Total or mean	**151.1**	**0.03**	**0.24**	**0.18**	**0.59**	-	-	**1.03**
	r		-	0.89	-0.73	-0.45	-	-	0.91
1999	64	126.8	0.06	0.05	0.07	0.22	0.7	0.2	0.40
	32	115.2	0.04	0.10	0.03	0.42	1.1	0.4	0.59
	14	90.5	0.02	0.01	0.06	0.31	0.7	0	0.40
	8	91.5	0.03	0.03	0.05	0.27	0.3	0	0.38
	Total or mean	**424**	**0.04**	**0.07**	**0.21**	**0.31**	**0.7**	**0.3**	**0.44**
	r		0.04 (0.76)	-0.85 (0.92)	0.97 (0.77)	-0.94 (-0.65)	-0.95 (0.08)	-0.76 -	-0.97 (1)

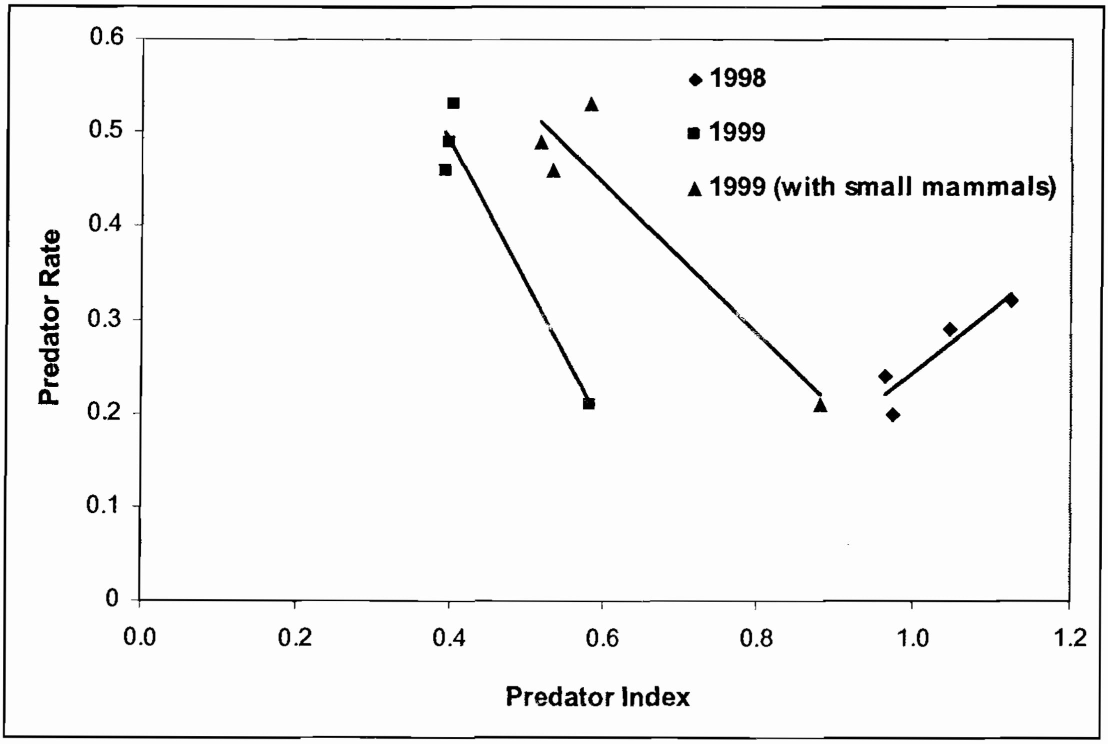


Figure 3.8 Relationship between the predator index (# observed/observer hour) and the predation rate for the natural nest stands.

Predation Rate and the Abundance of Songbirds

There was no significant relationship between the odds of predation on artificial nests (total predation on ground and shrub nests combined) and the abundance of ground and shrub nesting songbirds in either year (1998; F=0.010, df=23, p=0.92, $r^2 = 0.005$, 1999; F=0.19, df=23, p=0.67, $r^2=0.009$). Similarly, there was no significant linear relationship between the predation rate on natural nests and the abundance of ground and shrub nesting songbirds in either year (F=2.06, df=7, p=0.25), although linear trend lines suggest that in 1998 predation rate may have increased with residual tree density, but in 1999 it decreased (Figure 3.9). Neither was there a relationship between nest success and the abundance of ground and shrub nesting songbirds in either year (F=1.99, df=7, p=0.26), although in both years positive trends can be seen (Figure 3.9).

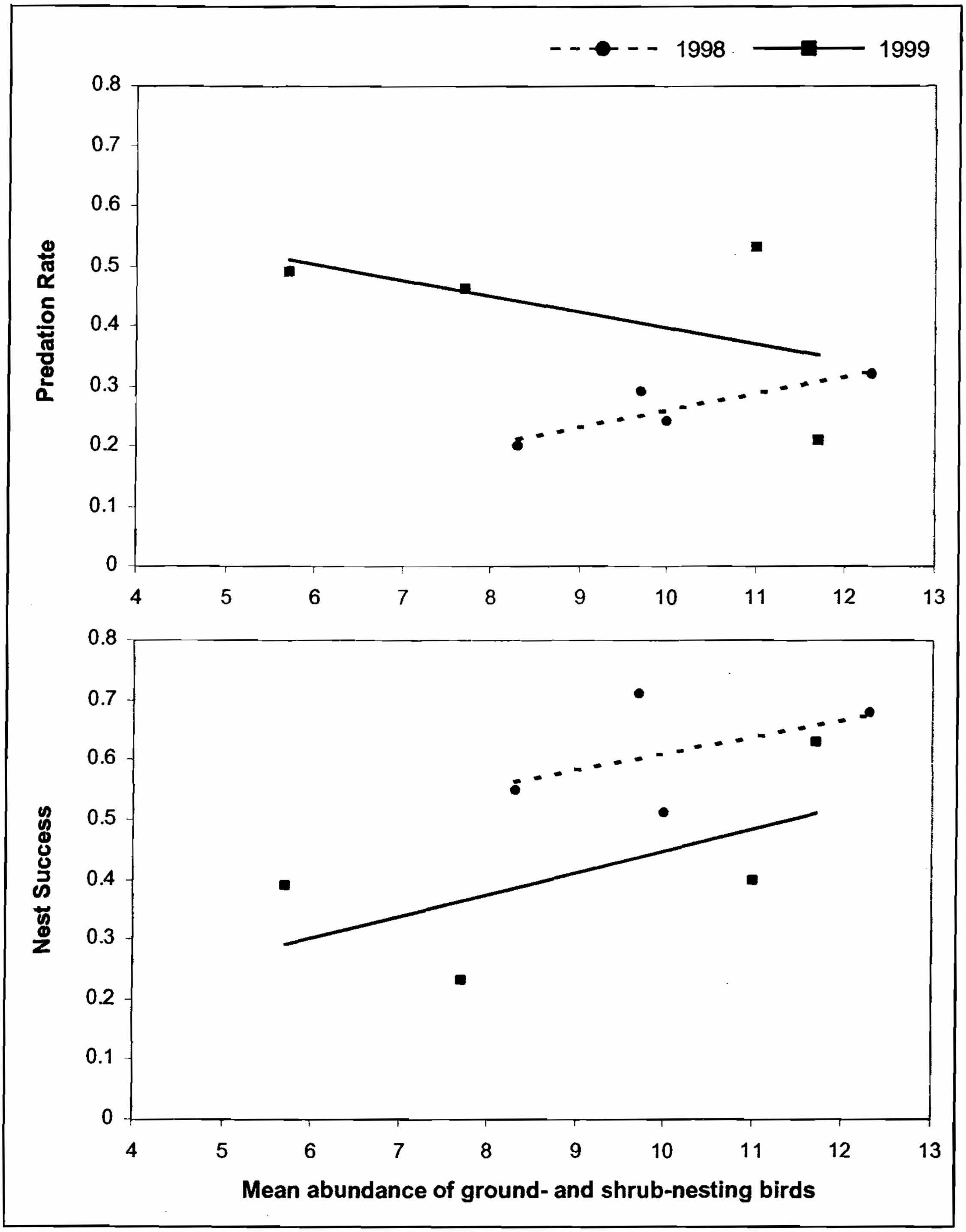


Figure 3.9 Relationship between the abundance of ground and shrub nesting birds and the predation rate and nest success, for the natural nest stands

Discussion

Predation on Artificial Nests in Relation to Residual Tree Density

I did not detect a strong or consistent influence of residual tree density on nest predation. Predation on artificial nests increased with residual tree density in logged stands, but only in one of the two years of the study. In burned stands there was no significant response in either year, with a positive trend in one year and a negative trend the next. The effect of residual tree density in logged stands was moderate in one year (1998), with a five-fold increase in residual tree density required to double the odds of predation. In 1999, an increase over 100-fold was required to produce a similar doubling in the odds of predation. In both years there was high variation among stands, reflected in the large confidence intervals around the effect size. In contrast to the results of Vega (1993), predation on ground and shrub nests in logged stands responded in a similar fashion to residual tree density.

Predation by birds showed the strongest and most consistent response to residual tree density, but again, this was only significant in logged stands. In 1998, a 5.6 fold increase in residual tree density led to a doubling of the odds of predation by birds, whereas a 10-fold increase was required to double the odds of predation by squirrels or small mammals. Although the effect was much weaker in 1999 (a 51-fold increase required to double the odds of predation), it was still much greater than that for other predator classes (> 100-fold for squirrels and > 1000-fold for small mammals). Predation by squirrels and small mammals also only increased in response to residual tree density in logged stands in 1998, although there was a trend in this direction for squirrels in 1999. Predation by small mammals was the only one to show a strong year effect, with predation nearly three times higher in 1998 than in 1999.

The response of predation by the different predator classes to residual tree density at the stand level was consistent with results at the nest level. Both ground and shrub nests depredated by birds were closer to residual trees than successful nests. There was a similar trend for squirrels, but not for small mammals.

To my knowledge, there have been only two other studies to directly examine the influence of residual trees on nest predation. Neither presents strong evidence of a strong effect. Vega (1993), working in Douglas-fir dominated stands in the Cascade Mountains of

Oregon, found higher predation on artificial nests in shrubs in green-tree retention stands (mean 47 %, range 18-83 % nests depredated) than in mature stands (6 %, 0-25 %) or clearcuts (24 %, 0-91%). For ground nests, however, predation was higher in clearcuts (38%, 8-77 %) than green-tree retention stands (17 %, 0-58 %). She attributed the higher predation on shrub nests in green-tree retention stands to Steller's Jays, which were more abundant in these stands. However, her study had several limitations: only Japanese Quail eggs were used, and thus small mammal predation could not be detected (Haskell 1995a), nests were exposed for only six days, less than the incubation time for most songbirds and less than the recommended exposure time (Ortega et al. 1998), there was a small sample size with only four stands of each type, and the study occurred in one week of one year only. There was very high variability among stands of each type, as the ranges of percent predation indicate. Given these limitations, her conclusion that green-tree retention stands may act as sinks (Pulliam 1988) for songbirds seems unwarranted.

Tittler and Hannon (2000) placed artificial nests in residual tree clumps in high and moderate retention stands and in mature forest controls in the aspen-dominated boreal mixed-wood forest. They reported nest predation was not related to the level of residual tree retention nor to the size of residual tree clumps, and concluded that elevated nest predation did not occur in green-tree retention cutblocks, for either ground or shrub nests. Although they did not census predator numbers, few jays or red squirrels were observed in their study area, which may in part explain their results.

Thus, there is neither strong nor consistent evidence that nest predation increases with residual tree density. The facts that 1) no effect was detected in an aspen-dominated ecosystem where jays and red squirrels exhibit low numbers, 2) an effect was detected in a coniferous ecosystem (this study) only in a year when red squirrel numbers were high, 3) predation by birds showed the strongest response to residual tree density in this study, and 4) nests predated by birds and squirrels were closest to residual trees in this study, suggest that the presence of an effect of residual trees on nest predation is directly linked to the number of jays and red squirrels in the area. This hypothesis should be tested by comparing predation rates in relation to residual tree density across a range of predator types and predator densities.

Differences in Nest Predation between Logged and Burned Stands

This is the first study, to my knowledge, to compare predation of artificial nests in logged and burned stands in relation to residual tree density. Results showed that response to residual tree density differed with disturbance type. In 1998, when nest predation increased with residual tree density in logged stands, there was no response in burned stands, and in 1999, when there was no significant response but a slight increasing trend in logged stands, there was a non-significant declining trend in burned stands. This pattern was generally consistent among the four classes of predators examined.

This difference suggests that burned stands had fewer predators that responded positively to residual trees than logged stands. This is consistent with the predator indices. Each of the four species of nest predators monitored in both burned and logged stands were detected at lower numbers and at a fewer number of stands in burned stands than logged stands. In particular, Gray Jays and red squirrels, thought to be important predators, were found at much lower abundance in burned stands. As discussed below, this may be due in part to the greater distance to mature forest in burned stands. To test this, comparisons of nest predation would have to be made between logged and burned stands of similar size and similar landscape composition, a difficult feat when most wildfires are much larger than logged stands.

Nest Predators and Patterns of Predation

Nest predators identified in this study were red squirrels, Gray Jays, deer mice, ground squirrels, and chipmunks. The strong correlation between the index of total abundance of predators (red and ground squirrels, Gray Jays, chipmunks, and deer mice) and the odds of predation on artificial nests suggests that it is likely that these species were largely responsible for the predation observed, and that other predators were not missed. Predation events by unknown predators and those in which the quail egg was missing and the plasticine egg left unmarked were thus likely due to the above species. However, patterns in nest predation were not clearly matched by those in the indices of predator abundance in artificial nest stands. Although red and ground squirrels, Gray Jays and chipmunks were detected more frequently in logged than burned stands, the odds of predation between the two disturbance types was similar. Nor were there consistent relationships between individual predator abundance and the odds of nest predation.

Red squirrels were more abundant in logged than burned stands, and in 1998 than in 1999, but there was no difference in predation by squirrels between years, nor between disturbance types. However, red squirrels also increased in abundance with the density of residual trees, as did squirrel predation in logged stands in one year. Surprisingly, the abundance of red squirrels was not correlated with the odds of predation by squirrels. The lack of matching patterns in red squirrel abundance and squirrel predation may in part be due to the fact that squirrel predation, as measured in this study, was composed of both ground and red squirrels because the marks left by these species could not be differentiated. Ground squirrels showed different trends than red squirrels, as they did not differ in abundance between years, and showed declining rather than increasing abundance with residual tree density.

Gray Jays also showed higher numbers in logged than burned stands, but, despite the fact that bird predation increased with residual tree density in logged stands in 1998, there was no relationship between Gray Jays and residual tree density. Possibly this is because detections of Gray Jays were very low. An analysis of Gray Jays in the 176 stands that formed the larger study (Chapter 2) showed a significant positive relationship with residual tree density (Appendix C). The correlation between the presence of Gray Jays and the presence of bird predation suggests this species was largely responsible for bird predation. Black-capped Chickadees have been suggested as nest predators, as they have been observed pecking at the eggs of other birds (Pribil and Picman 1994). Although this species was fairly common in the study area (Chapter 2), most of the marks attributed to birds (3mm) were larger than a chickadee bill.

Small mammal predation was high in this study, comprising about half of the total predation in 1998 and one third of total predation in 1999. In 1998, predation on artificial nests by small mammals was 3-8 times higher than predation by any other class (including unknown). In 1999, it was equal to unknown cases, and only 2-4 times higher than any other class. This suggests that small mammal numbers were much higher in 1998 than 1999, or that small mammal numbers were similar in both years but they depredated more nests in 1998. Unfortunately small mammal trapping was only conducted in 1999 so I cannot differentiate between the two. Observational data suggested that chipmunk numbers were similar in each year, so if there was a change in small mammal numbers it was likely due to changes in the abundance of deer mice or red-backed voles rather than chipmunks. Both mice and voles are known to exhibit high annual variability (3-5 fold, Banfield 1974).

Unfortunately, the markings left on plasticine eggs by chipmunks and deer mice were similar, and red-backed voles left no marks, making it impossible to determine which species was responsible for most of the predation. However, deer mice were the only species of the three to show a correlation between abundance and the odds of predation by small mammals. Deer mice also showed a slight positive relationship with residual tree density, as did predation by small mammals, whereas the other species did not. The role of *Peromyscus* as nest predators is not clear. Deer or white-footed mice are frequently captured in photographs at artificial nests, and have been observed eating both zebra finch and house sparrow eggs in captive trials (Maier and DeGraaf 2001). However, predation of actual songbird eggs by mice in the wild has not, to my knowledge, been confirmed (Maier and DeGraaf 2000). Deer mice were suspected as predators of Prothonotory Warblers (*Protonotaria citrea*, Guillory 1987), and Maxson and Oring (1978) found that predation on Spotted Sandpiper (*Actitis macularia*) eggs was virtually eliminated once *Peromyscus* were trapped out of the study area, indirectly implicating mice as nest predators.

Neither the abundance of chipmunks nor of red-backed voles showed any relationship with the odds of small mammal or squirrel predation, suggesting that neither of these species played a major role in nest predation, that the likelihood of predation is not related to the density of these predators, or that the indices of abundance were inaccurate. This lack of correlation is consistent with the diet of these species. Chipmunks (both least and yellow pine) are mainly herbivores, eating eat primarily seeds, berries, nuts, and insects, although they have been reported to occasionally take bird eggs or young birds in the nest (Banfield 1974), and diet studies have revealed avian remains in the gut contents of chipmunks (Maier and DeGraaf 2000). Red-backed voles eat primarily leaves, buds, fruits and forbs (Banfield 1974). They are less commonly photographed at nests than chipmunks or deer mice, although Cotterill and Hannon (1999), Sieving and Willson (1998), and Fenske-Crawford and Niemi (1997) obtained photographs of them at artificial ground nests. However, although they were photographed in direct contact with the eggs, the voles never removed or damaged eggs. Only one study reports vole predation on actual eggs or nestlings (Bures 1997). Voles are one of the dominant species in montane and northern forests, and thus have the potential to be play a large role in nest predation, but more data is needed before they can be clearly identified as nest predators.

Other studies also have found predator abundance does not consistently match amounts or patterns of predation. Cotterill and Hannon (1999) reported trends in predation rates to match those in the abundance of the dominant predators in or near the study area. Sieving and Willson (1998) observed that red squirrels exhibit habitat associations consistent with the major pattern of predation on artificial nests and found that nest predation declined in parallel with squirrel density (see also Bayne and Hobson 1997, but see Boulet et al. 2000). However, Bayne et al. (1997) reported that, although red squirrel densities in mixedwood and conifer forests were similar, predation rates on artificial nests were higher in the conifer forest.

There may be several reasons why patterns of predation on artificial nests were not clearly matched by patterns in predator abundance in this study. First, the indices of abundance may have not reliably represented actual abundance of the predator species. This is particularly likely for ground squirrels and chipmunks, whose indices of abundance were based on observations made in the field. Although observational data can reliably represent patterns in population changes (Hochachka et al. 2000), in my study the index was based on a small number of hours of observations. The index of abundance of Gray Jays was also likely poor, as this species does not give territorial vocalizations, often travels in family groups, and thus is poorly censused by point counts. However, the point counts should have provided a reliable index to the abundance of red squirrels, as they animals give easily detected territorial calls.

Second, landscape characteristics may be a stronger driver of abundance of predators such as red squirrels and Gray Jays than are stand characteristics. For example, Boulet et al. (2000) found depredation on artificial nests by red squirrels increased as spruce cover increased in a boreal forest landscape. Similarly, Song and Hannon (1999) found predation on artificial shrub nests increased with increasing conifer cover and decreasing deciduous cover within a 450 m radius of the nest. In my study, logged stands were generally adjacent to or surrounded by mature forest. In contrast, burned stands were located in large (2845-16,676 ha) severe wildfires, generally more than 1 km from mature forest. Both red squirrels (Rusch and Reeder 1978, Kemp and Keith 1970) and Gray Jays (Campbell et al. 1997) generally reach their highest densities in mature coniferous forest. Detections of both species, especially Gray Jays, were rare in the study stands. If these predators forage opportunistically on bird nests in young stands, predation would be expected to be higher in stands closer to mature forest.

Third, none of the major predators are known to specialize on predation of bird eggs or nestlings. Although red squirrels can kill adult passerine birds (Sullivan 1991) and may be aggressive predators when they encounter bird nests containing eggs or nestlings (Sieving and Willson 1998), their main food is fungi and the seeds of conifer trees (Rusch and Reeder 1978). Similarly, although Gray Jays have been observed carrying songbird nestlings (Cotterill and Hannon 1999) and may be capable of specializing on nests (Andrén 1992, Strickland and Ouelett 1993), they eat primarily insects, fruit, and carrion (Ehrlich et al. 1988). Both predators tend to prey opportunistically (Angelstam 1986). In this study, red squirrels were more abundant and detected in more stands than Gray Jays, but birds preyed on a higher percentage of nests than squirrels. This implies jays eat more eggs or are greater 'egg-specialists' than squirrels, which was also suggested by Boulet et al. (2000).

Concealment and the Influence of Vegetation on Nest Predation at Natural Nests

Numerous studies have reported a positive relationship between nest survival and concealment, with predation rates lower at nests with greater concealment in 29 of 36 studies reviewed by Martin (1992). In my study, for both artificial and natural nests, depredated nests were significantly less concealed than successful nests, but only for nests placed in shrubs. This difference between ground and shrub nests may relate to the differences in dominant predators on each nest type. Small mammal predation was higher on ground than shrub nests, while bird predation was higher on shrub than ground nests. Small mammals, the majority of which were likely mice, are nocturnal predators that use olfactory cues to find nests (Howard et al. 1968). Thus, concealment would not be expected to be a predictor of nest predation for ground nests. In support of this, Rangen et al. (1999) found that mice destroyed well-concealed nests. In contrast, Gray Jays are diurnal predators known to visually detect nests by scanning from perches (Strickland and Ouelett 1995). Clark and Nudds (1991) reviewed 38 studies, and found that the importance of nest concealment to nest success was dependent upon the predator community. For ducks, concealment was only important when the principle predators were avian, as compared to when they were mammalian or a combination of mammals and birds. Similar conclusions appear to apply here.

For natural nests in this study, none of the means of the other vegetation variables measured around the nests differed between depredated and successful nests. I had expected nests surrounded by greater vegetation cover to be less susceptible to predation. Martin (1993b) postulated that increased structural heterogeneity of vegetation around nests decreased the risk of predation, because increased vegetation decreases the transmission of olfactory, visual, and auditory cues to predators. Martin (1993b) also suggested that since birds do not nest randomly, it benefits predators to search the vegetation types that represent potential sites for prey. A greater number of vegetation types should decrease the search efficiency of the predators, and decrease predation rates. The lack of association between vegetation and nest success in this study may be due to 1) small sample sizes, 2) stand-level factors overriding nest-level factors, 3) the overriding importance of concealment as the main vegetation factor influencing predation, 4) the variety of predators preying on nests, each selecting for different nest characteristics, 5) the potentially random nature of predation, or 6) factors other than nest success influencing nest site selection.

Birds may select nest sites for various reasons other than protection from predators; nest sites with specific microclimates may be selected to provide protection from inclement weather and favorable conditions for the thermoregulation of eggs and developing young (Calder 1973, in Matsuoka et al. 1997), to minimize the prevalence of brood parasites (Robinson 1992) or nest ectoparasites, or to be in close proximity to an adequate food supply (Holmes et al. 1992). In this study, losses of natural nests to inclement weather equaled that lost to predation in one year. Thus, birds may be balancing predation risk with protection from inclement weather. Ground-nesting songbirds that require dense foliage for thermal reasons or protection from predators other than mice may face a trade-off between thermoregulation or avoidance of non-mouse predators and mice predation (Martin 1988), reinforcing the idea that birds face multiple selection pressures from the predator community alone (Rangen et al. 1999).

This study did not detect differences in overall predation rates or patterns between ground and shrub nests, for either artificial or natural nests, although there was a trend for depredated natural shrub nests to be closer to the ground than successful shrub nests. Results from other studies are inconsistent. Some studies on artificial nests have found that predation on shrub nests is higher than that on ground nests (Reitsma and Whelan 2000, Song and Hannon 1999, Seitz and Zegers 1993, Yahner and Scott 1988), or that successful nests were closer to the ground than depredated nests (Rangen et al. 1999). However, other artificial nests studies found no difference in predation on ground and shrub nests (Bayne and Hobson 1997, Wilcove 1985, Best and Stauffer 1980) or that predation was higher on ground nests (Cotterill and Hannon 1999). Martin (1993a), in a review of nesting success of neotropical migrants, reported that natural shrub nests in forested habitats typically suffer higher predation rates than ground nests, while the opposite appears true in shrub and grassland habitat. It is likely that relative levels of predation depends on the composition of the predator community.

Comparison of Predation on Artificial and Natural Nests

Artificial nests were depredated at higher rates than natural nests, consistent with the findings of other studies in forests (King et al. 1999, Sloan et al. 1998, Wilson et al. 1998, Reitsma et al. 1990, Storaas 1988, but see Ortega et al. 1998 for evidence that this relationship depends on the length of time nests are exposed). Of more importance, however, is that patterns of predation I observed were not consistent for artificial and natural nests. Predation on natural nests was higher in 1999 than in 1998, while for artificial nests the reverse was true. The amount of predation on natural nests did not increase significantly with residual tree density in 1998 as it did for artificial nests, although there was a trend in this direction. However in 1999 results from the two nests types were similar as predation did not increase with residual tree density for either nest type. Similarly, for both nest types, nest concealment was lower for depredated shrub nests than successful shrub nests, but similar between depredated and successful ground nests.

This inconsistency in the patterns of predation between artificial and natural nests has been found in the few other studies that have compared the two. Sieving and Willson (1998) reported opposite patterns of nest predation between artificial and natural nests; natural nests suffered greater losses in deciduous than coniferous forest, while artificial nests had higher losses in coniferous forest. Similarly, Fenske-Crawford and Niemi (1997) found higher rates of predation along edges in a forest-dominated landscape, but a concurrent study on an adjacent site found no edge effect for natural nests (Hanski et al. 1996). Fenske-Crawford and Niemi (1997) suggested that the difference in results was because the artificial nests were mainly on the ground while the natural nests were mainly above ground. In a grassland ecosystem, Davison and Bollinger (2000), found patterns of predation on wicker nests to be very different from those on natural nests, while patterns of predation on more realistic looking grass nests were more similar, suggesting the realism of artificial nests may be an important factor. One study did find similar trends: Wilson et al. (1998) found predation rates on artificial nests to decrease as forest patch size increased, similar to the pattern reported for Wood Thrush (*Hylocichla mustelina*) on the same sites.

In this study, differences in concealment may in part explain the higher predation on artificial than natural nests. Concealment of artificial shrub nests was substantially lower than that of natural shrub nests, and slightly lower for artificial ground nests than natural ground nests. As discussed previously, Gray Jays are visually oriented predators that may locate artificial nests more easily than natural nests because of their lesser concealment (Davison and Bollinger 2000, Sullivan and Dinsmore 1990). King et al. (1999) also reported artificial nests to be more conspicuous than natural nests, but that conspicuousness alone did not account for the higher predation on artificial nests.

Differences in composition of the predator community may also explain differences in predation patterns between artificial and natural nests. Although there were similar or greater detections of ground squirrels and chipmunks in stands with natural nests than in stands with artificial ones, there were fewer detections of the species more likely to be important nest predators; red squirrels, Gray Jays, and deer mice. Considering that there were relatively good correlations between these predators and the predation rate on artificial nests, lower predation on natural nests could be expected. Finally, differences in the rate and pattern of predation on artificial and natural nests could also simply be due to the small sample size of natural nests. While results from artificial nests were based on 693-697 nests in 24 stands each year, results from natural nests were based on 33-39 nests in four stands each year.

Other factors that have been proposed to cause differences in patterns of predation between artificial and natural nests include use of unrealistic looking wicker baskets for nests (Davison and Bollinger 2000), human-associated smells and activity around artificial nests (Willebrand and Marcström 1988), deployment of nests in different densities, spacing, or microhabitats than natural nests (Major and Kendall 1996, Martin 1993b), nest defense by adults at natural nests (Montgomerie and Weatherhead 1988), and use of Japanese Quail or plasticine eggs rather than natural songbird eggs. In this study, realistic grass nests that closely resembled those of songbirds nesting in the study area were used as artificial nests, and there were likely no more human smells and activity around artificial nests than natural ones. If anything, there was more activity around natural nests as these were visited every 2-4 days rather than every six days. Artificial nests were placed at higher densities than typically found in the study area (13.3/ha) than natural nests (1-5/ha). However, no trends in the amount of predation and the abundance of songbirds were detected, suggesting this is an unlikely reason for why predation rates were higher on artificial nests. The presence of parents at the nest could both increase or decrease predation risk, and cannot be discounted as a factor. During incubation the female may provide additional concealment to the nest through her cryptic plumage (Martin 1993a), and parents have been found able to drive away nest predators (Cresswell 1997). On the other hand, cues given by parents near the nest (movement, sounds, scent) may increase predation by mammals (Vickery et al. 1992b) and birds (Storaas 1988, Willebrand and Marcström 1988).

The use of quail and plasticine eggs may be an important factor in explaining the differences between natural and artificial nests. Artificial nest studies have been criticized for using Japanese Quail eggs (Haskell 1995a), as these eggs are too large and thick-shelled for small mammal predators to break open (Rangen et al. 2000, DeGraaf and Maier 1996, Roper 1992, but see Craig 1998). Despite the fact that considerably smaller Chinese Painted Quail eggs were used in this study rather than Japanese Quail eggs, there was no evidence that small mammals could open these eggs. Despite their smaller dimensions than Japanese Quail eggs, the Chinese Painted Quail eggs were still larger than the eggs of several of the smaller songbirds in the study area, and had thicker shells than actual songbird eggs (pers. obs). This finding is consistent with results from studies that have compared predation on the two eggs types, which report rates of predation on Button Quail (*Turnix* sp., similar in size to Chinese Painted Quail eggs) and Japanese Quail eggs to be similar (Lewis and Montevecchi 1999, Sieving and Willson 1998). Thus, without the use of plasticine eggs, or interpreting scratches as predation events, predation by small mammals would have been underestimated in this study. Plasticine eggs are likely a better choice than using scratches, as quail eggs may be unknowingly scratched prior to placement in the field, and scratches are often difficult to detect (pers. obs.). However, nests with plasticine eggs have been found to have higher depredation rates than nests with only real eggs (Maier and DeGraaf 2001, Rangen et al. 2000). Rangen et al. (2000) speculated that the odor of the plasticine was responsible for the preferential depredation of plasticine eggs, while Maier and DeGraaf (2001) suggested it was due to the behavioral tendency of mice to nibble objects as they gather olfactory cues and to gnaw at hard objects, eventually shaving a hole. Zebra Finch (*Taeniopygia guttata*) eggs have been proposed as an alternative to quail eggs (Rangen et al. 2000), but studies have shown these eggs to be breached more often than house sparrow eggs, likely due to their smaller size and thinner shells (Maier and DeGraaf 2001). Thus, studies using these may overestimate predation rates by small mammals.

The documentation of small mammals at artificial and natural nests (this study, Bayne and Hobson 1997, DeGraaf and Maier 1996, Reitsma et al. 1990), their demonstrated ability to consume small passerine and clay eggs (Maier and DeGraaf 2001, DeGraaf and Maier 1996, Nour et al. 1993, but see Maier and DeGraaf 2000) and their widespread distribution across habitats (Banfield 1974), suggests small mammals may be significant predators on nesting songbirds. Not considering marks in the clay eggs to be predation could exclude a large component of the predator community and create misleading results (Bayne and Hobson 1999, Haskell 1995b, Roper 1992), especially if predator communities differed among the habitats being evaluated. In conclusion, using either plasticine or zebra finch eggs may overestimate the amount of predation by small mammals, but not using them will definitely underestimate it.

The extent of predation on natural bird nests by mice and chipmunks is unknown, and needs to be determined in order to interpret the results from artificial nest studies. Rigorous experiments should be done where mice are removed from experimental areas and nest predation monitored both prior and following, with adequate controls for temporal changes in small mammal numbers. Remote cameras or hair catchers could also be established at nest sites and predators identified.

Due to the difficulty of finding high numbers of natural nests, artificial nests will likely continue to play an important role in the studies examining factors influencing nest predation and nest success. The differences in amounts and patterns of predation between artificial and natural nests found in this and other studies suggests that results from artificial nest studies must be interpreted with caution, particularly if the study sites differ in the composition and abundance of predators. Ideally, artificial nest experiments should be used as preliminary studies or to generate hypothesis, but conclusions arising from them, particularly ones with strong implications for conservation, should be confirmed with natural nests. Many nest predation studies are only conducted for one year. The difference in results from one year to the next found in this study suggest nest predation studies be conducted over multiple years.

Management Recommendations

Since this study did not find any strong or consistent evidence that residual trees increase predation on ground or shrub nesting songbirds, managers should not avoid variable retention prescriptions for this reason. However, a moderate increase in nest predation in stands with higher densities of residual trees is possible in areas or years when numbers of red squirrels and jays are high. In this study, in the year that red squirrel abundance was high, the risk of predation on artificial nests doubled with a five-fold increase in residual trees. Based on the range of residual tree densities in this study, doubled predation risk occurred at residual tree densities of 40 trees/ha and greater. However, the high variability among stands and the large confidence interval around the estimated effect size found in this study suggest that magnitude of the effect may vary greatly.

Many factors in addition to the risk of nest predation to ground and shrub nesting songbirds need to be considered when considering variable tree retention prescriptions. Residual trees in harvested stands are associated with a strong increase in the use of those stands by many mature forest birds (Chapter 2). Other species, including nest predators such as red squirrels, Gray Jays and Steller's Jays, also have been shown to increase use of stands with residual trees relative to clearcuts (Vega 1993, Appendix C). These species may be at greater risk from forest management practices than many ground and shrub nesting songbirds, which can benefit from the creation of early seral habitat through logging (Chapter 2). Other hypothesized benefits of retaining residual trees in managed forests include maintenance of tight nutrient cycles, refugia and inocula for nonvagile mycorrhizae and nitrogen-fixing bacteria, beneficial predator-prey relationships among forest invertebrates, habitats for vascular plants and vertebrates that require either structural complexity and/or late-seral stands, and dispersal opportunities for species that avoid forest openings (Franklin et al. 1997, Hansen et al. 1995a). There may also be social benefits in regions where the public is strongly against clear-cutting.

Thus, in most areas, it is likely that the overall benefits of retaining variable densities of residual trees will outweigh the possible increased risk of nest predation on ground and shrub nesting birds. An exception may be made for cases where specific ground- or shrub-nesting bird species are threatened or at very low numbers.

CONCLUSIONS

Summary

This is the first study, to my knowledge, to compare abundance, richness, structure, and nest predation of songbird communities within post-harvest and post-wildfire stands in relation to residual tree density and type. Results showed that, although some individual species responded differently to disturbance types, in general the songbird communities in young burned and logged stands were similar. Logged and burned stands had similar dominant species, evenness, and diversity of birds, although logged stands had higher mean richness and abundance than burned stands. There were no species detected in burned stands that were not also detected in logged stands. Of 26 species examined statistically, 20 showed higher abundance in logged stands or no difference in abundance between logged and burned stands. Six species showed higher abundance in burned stands than logged stands: Cassin's Vireo, Northern Flicker, Red-breasted Nuthatch, Townsend's Solitaire, Western Tanager, and Yellow-rumped Warbler (see Appendix A for scientific names). Differences in the songbird communities between logged and burned stands are likely related to differences in the vegetation between the two disturbance types. Logged stands had greater shrub cover, shrub richness, basal area of broadleaf trees, densities of residual conifer understory trees, and number of vertical vegetation layers, but fewer numbers of regenerating pine trees, snags and pieces of down wood.

It is critical to recognize that the results of this study are based on a comparison between stands burned by severe wildfires and stands managed primarily in a non-intensive fashion. Many of the logged stands in this study, particularly those harvested prior to the early 1980's, were harvested in a 'sloppy' fashion, leaving numerous residual trees and parts of large logs. Often these stands were not planted, but left to regenerate naturally, resulting in mixed species stands with high horizontal and vertical structure. These practices also resulted in high variability among stands. Had more intensively managed stands, with few residual conifer or broadleaf trees, little shrub cover, predominantly pine regeneration, and simple vertical and horizontal structure been examined, conclusions would likely have been very different.

As time-since-disturbance increased, the bird communities in burned and logged stands became more similar in the higher elevation biogeoclimatic subzone, the ESSFdk (hereafter ESSF), but not in the lower elevation MSdk (hereafter MS). In the ESSF, characteristics of the vegetation became more similar through time, with the exception of the density of regenerating pine trees. In contrast, in the MS, differences in the density of residual conifer overstory trees and in the density of regenerating conifer trees became greater through time. Higher retention levels of residual trees did not lead to greater convergence between burned and logged stands as has been suggested (Lee et al. 1999).

Both the density and type of residual trees strongly influenced songbird species richness and total abundance. Richness and total abundance were significantly associated with the density of residual broadleaf trees in the MS and with the density of residual conifer understory trees in the ESSF. Residual tree density also significantly influenced the abundance of individual species, entering into 22 of 24 species models in the MS and 12 of 20 models in the ESSF. Residual conifer overstory trees (>19 cm dbh) were strongly associated with 16 of the 24 species examined in the MS: nine positively and seven negatively. Species negatively associated with residual overstory tree density were generally those that feed or nest on or near the ground in open shrubby habitats, such as the Dark-eyed Junco, American Robin, and MacGillivray's Warbler. Species with the strongest positive responses were a mix of those preferring open forest stands with large canopy trees (Western Tanager and Cassin's Vireo) and those reaching their higher densities in older closed canopy forests (Townsend's Warbler, Golden-crowned Kinglet). Associations with conifer understory trees (< 19 cm dbh) tended to be positive in the ESSF (five of six species) and negative in the MS (seven of ten species). Associations with broadleaf trees were uniformly positive, with the exception of the Yellow-rumped Warbler.

There was no strong or consistent evidence that predation on nests of ground and shrub nesting songbirds increased in association with the density of residual overstory conifer trees. Predation on artificial nests increased moderately with residual tree density in logged stands, with a five-fold increase in residual tree density required to double the odds of predation, but only in one of two years. In burned stands there was no significant response in either year, with a positive trend in one year and a negative trend the next. In both years there was high variation among stands.

The main nest predators were red squirrels (*Tamiasciurus hudsonicus*), Gray Jays, deer mice (*Peromyscus maniculatus*), ground squirrels (*Spermophilus spp.*), and chipmunks

(*Eutamius spp.*). There was a significant correlation between the index of abundance of all predators and the total amount of nest predation, but patterns in nest predation were not clearly matched by those in the indices of individual predator abundance. Although most predators were detected more frequently in logged stands than in burned stands, the odds of predation between the two disturbance types was similar. Predation by Gray Jays, and to a lesser amount red squirrels, showed the strongest and most consistent response to residual tree density.

Artificial and natural nests differed in the amount and pattern of predation, although the sample size of natural nests was low. In both years artificial nests were depredated at higher rates than natural nests. Predation on natural nests was higher in 1999 than in 1998, while for artificial nests the reverse was true. The amount of predation on natural nests did not increase significantly with residual tree density in 1998 as it did for artificial nests, although there was a trend in this direction. In 1999 results from the two nest types were similar as predation did not increase with residual tree density for either nest type.

Management Recommendations

Results from this study show substantial benefits of variable retention for songbirds. Retaining even a low density or proportion of the volume of trees in logged stands can significantly increase richness and abundance of the songbird community using those stands. Songbird response is dependent on both the type and density of residual trees, with broadleaf trees and understory conifer trees having the greatest association with overall richness and abundance, and overstory conifer trees having the greatest influence on abundance of forest birds that nest or forage in mature forest stands. Because individual species responded both positively and negatively to residual trees, a variety of residual tree densities throughout the landscape will be needed to provide adequate habitat for most species of songbirds. Although this study did not examine distributions of residual tree density throughout the landscape that would provide optimal habitat value for songbird populations, the data could be used to develop models addressing this issue. It should be noted that the response of species associated positively with residual tree density was generally greater than the response of those associated negatively. For example, for a given elevation and stand age, doubling the density of overstory residual trees in logged stands in the MS was associated with a 2.06 fold increase in abundance of Swainson's Thrush, and only a 0.08 fold decrease in abundance of

Orange-crowned Warbler. Thus, leaving higher densities of residual trees should benefit birds nesting and foraging in tree canopies, without unduly decreasing the abundance of ground- and shrub-foraging and nesting species. The lack of a strong or consistent influence of residual trees on nest predation suggests that managers should not avoid variable tree prescriptions for this reason.

To answer the question 'how many trees should be retained in logged stands?' requires some reflection. In comparison to wildfire, the natural disturbance baseline, most (20 of 26) of the songbird species examined in this study reached higher or similar abundance in logged stands as compared to burned stands. This suggests that the residual tree characteristics of the stands in this study provided adequate habitat for the majority of songbird species. Thus, in the MS, a mean density of 56 within a range from 0 – 238 trees/ha of western larch, Douglas-fir and/or white spruce >19cm dbh, and a mean density of 53 within a range of 0 - 236 trees/ha <19cm dbh of the same species above, in combination with retaining all broadleaf trees, can serve as a rough guide to retention levels appropriate for most songbirds. In the ESSF, a mean density of 75 within a range of 0 - 120 trees/ha of Engelmann spruce, subalpine fir, Douglas fir, or western larch <19cm dbh and a mean density of 5 within a range of 0- 36 trees/ha of those species >19cm dbh can indicate retention levels appropriate for most songbirds. Lodgepole pine was rarely left as a residual tree in this study area, and associations between it and songbirds may be quite different than for those tree species above.

Ranges of residual tree density are provided in addition to means because the positive and negative association of songbird species with residual tree density imply that variable densities of residual trees throughout the landscape are needed in order to provide good habitat for a variety of bird species. Simply leaving a target mean residual tree density in all stands will not provide habitat for all members of the songbird community. Considering the previous argument, which suggests greater benefits to the songbird community as a whole at moderate to higher residual tree densities, and the fact that some residual trees will blow over in the first few years following harvest (pers. obs.), I suggest managers focus on the medium to high ends of these ranges, rather than the low end. Since the ranges above represent little volume of timber (mean basal area retention in the MS was 4 m^3/ha), there should be little direct economic impact from this recommendation. However, higher densities of residual trees have been shown to influence the growth of regenerating coastal Douglas-fir stands in the Pacific Northwest (Acker et al. 1998, Rose and Muir 1997). Studies are needed to determine if and at what level this occurs in dry interior forests.

However, use of the natural disturbance baseline also indicated that there were six species whose abundance was lower in logged than in burned stands, primarily in the MS. This suggests that logging practices need to be modified to provide better habitat for these species. As these six species were all either cavity nesters or species preferring open forest habitat, the densities of both snags and residual overstory trees will need to be increased in logged stands above the densities seen in this study. Increasing the number of snags typically used by cavity-nesting birds in this study (western larch, Douglas-fir, broadleaf trees with mean dbh 40cm, min dbh 20cm, and >5m tall) should improve habitat for these species. This will also provide habitat for other, non-songbird species such as bats and owls (Bunnell et al. 1999). For birds preferring open forest habitat, the residual tree characteristics of the burned stands in which these species showed highest abundance can be used as a guide. These species were not detected in areas that burned severely, but in stands with high densities of large, live residual Douglas-fir and western larch trees and few understory trees. Emulating these stand characteristics and producing timber volume will be difficult, thus retaining patches of large diameter trees as reserves may be the best strategy to maintain habitat for these species.

In addition to residual tree levels, other characteristics of the vegetation, such as shrub cover and vegetation layers, should be considered. Although this study did not examine relationships between songbirds and vegetation other than residual trees, the higher shrub cover, shrub richness, and number of vegetation layers present in logged stands likely contributed to the higher richness and abundance of songbirds in these stands (e.g., Bunnell et al. 1999, Willson 1974, MacArthur and MacArthur 1961). Forest management practices that create and maintain multi-layered stands with good shrub cover (mean 50%, SD ±20%) will thus likely benefit the songbird community as a whole. It follows that forest management practices that decrease shrub cover, shrub richness and vertical complexity will likely result in reduced bird species richness and abundance.

The recommendations above are designed to address songbird habitat, and may not provide habitat for other taxa (e.g., Martin and Eadie 1999). The lack of differences observed in the structure of the songbird communities in burned and logged stands, despite significant differences in the vegetation, suggest that the songbird community may not be particularly sensitive to habitat changes induced by forest management. This idea is supported by the findings of a recent review on the long-term effects of forestry on boreal birds in Fennoscandia and Canada (Imbeau et al. 2001). While forestry is the main cause of threat for 9.4% of the 32 species of threatened birds in Fennoscandia, it is the main cause of threat for

26.6% of the 759 endangered species of invertebrates, and 53% of the 374 threatened species of fungi and lichens (Imbeau et al. 2001). Among birds, it has been suggested the resident habitat specialists such as the woodpeckers, rather than migrants, are most likely to be sensitive to the large scale changes in habitat occurring from forest management (Hunter 1992, Wiens 1994). Neotropical-temperate migrants are probably relatively plastic in their habitat requirements, as indicated by their ability to survive in both temperate forest and tropical ecosystems (Hunter 1992).

The Natural Disturbance Approach to Forest Management

This dissertation was prompted by questions surrounding use of the concept of emulating natural disturbances as an approach to forest management. Can naturally disturbed areas be used as baselines for managed areas ? Should managers attempt to emulate natural disturbances as closely as possible ? Should management goals be based on natural disturbance regimes ?

By itself, this study cannot fully answer these questions, but some conclusions can be drawn. Results suggest that using naturally disturbed areas as a baseline for assessing the impacts of forest management is a highly useful approach. By using stands burned by wildfire as a 'control' for stands that were logged, species at risk from past logging practices were identified, as were components of the vegetation that could be manipulated to improve habitat for these species in managed forests. Results also suggested that most of the common early seral songbird species in the study area are not at risk from past, non-intensive logging practices, and in fact may have enhanced numbers over those found in a stands affected by wildfire. The fact that the vegetation in logged and burned stands differed in many respects, but the songbird communities in both disturbance types were similar, suggests that the system can vary from a 'natural disturbance baseline' and still retain the integrity of the songbird community. However, as increasing emphasis is placed on intensifying stand-level forest management practices, for example by achieving conifer canopy closure as quickly as possible and reducing broadleaf tree and shrub cover, maintaining habitat for songbirds will become a much greater challenge.

Results also emphasize that, at the stand level, variability in residual tree density is linked to the integrity of the songbird community. Simply managing to one target residual tree density and type will not provide adequate habitat for all songbird species in the community. Managing for ranges rather than target means will require closer tracking of residual tree density and type than currently practiced, and consideration of past practices in deciding future ones. Managing for biocomplexity in a regulatory environment, although difficult, is an issue that must be addressed if biodiversity is to be maintained in managed forests.

This study examined only one of the three axes describing natural disturbance regimes – severity. Without considering the rate of return or the size and spatial distribution of disturbance, efforts to maintain songbird communities or biodiversity in managed forests are unlikely to be successful. As this study has shown, stands with higher densities of residual trees can provide at least foraging habitat for many species typically associated with mature and old forest. However, some species associated with old forest, (e.g. Varied Thrush, Brown Creeper) were rarely detected in this study. Since these species are moderately abundant in older forests in the study area (unpubl. data), this suggests the residual tree densities in this study were not high enough to provide habitat for these species, or that these species require aspects of mature and old stands not found in young stands with residual trees. It is likely that stands of mature and old trees, reserved or managed on longer rotations, or partial cut stands with low volume removal, will be required to provide habitat for such species.

How closely managers should attempt to emulate natural disturbance patterns is a more difficult question. As a society we demand many values from our forests, including timber production, wildlife habitat, water quality, recreational opportunities, and spiritual retreats. Forest landscapes in which natural disturbance regimes are allowed to operate without hindrance (i.e. no fire suppression) are unlikely to provide for all of these values. Certainly, in my study area, where severe wildfires frequently burned entire valleys, closely mimicking natural disturbance through logging would likely lead to public outcry, diminished recreational opportunities, and an irregular flow and lesser amount of wood products. Mimicking the severity, size and rate-of-return exactly would also be impossible logistically and politically.

Rather than simply trying to mimic natural disturbance regimes as closely as possible, a clear understanding is needed of the consequences of different degrees and types of deviation from them. This requires an understanding of cause-and-effect relationships, or how species respond to disturbance and variability in the landscape. In virtually all landscapes a compromise must be struck between natural processes and societal demands (Swanson et al. 1993). The challenge is determining which components and processes of natural disturbance regimes are critical, how much of the range of natural variability must be maintained, and how closely natural disturbance regimes must be emulated in order to sustain species and ecosystems. Increased understanding of the processes that have shaped and will continue to shape ecosystems will aid in the design of management activities that work in concert with, rather than counter to, these processes (Morgan et al. 1994).

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APPENDICES

APPENDIX A

COMMON AND SCIENTIFIC NAMES, MIGRATORY STATUS AND NEST LOCATION OF BIRDS DETECTED IN THE STUDY AREA

Table A.1 Common and scientific names (after BC Ministry of Sustainable Resource Management 2001) for all bird species detected in study area, along with their migratory status (resident, short-distance or neo-tropical migrant) and primary nesting location (following Campbell et al. 2001, Campbell et al. 1997, Ehrlich et al. 1988 and personal observation in the study area). RES: resident, SDM: short-distance migrant, NTM: neotropical migrant. Species that undergo elevational migrations only were classified as residents.

Common Name	Scientific Name	Status	Nest Location
Canada Goose	*Branta canadensis*	SDM	Ground
Northern Goshawk	*Accipiter gentilis*	RES	Tree
Red-tailed Hawk	*Buteo jamaicensis*	SDM	Tree
American Kestrel	*Falco sparverius*	SDM	Cavity
Ruffed Grouse	*Bonasa umbellus*	RES	Ground
Spruce Grouse	*Falcipennis canadensis*	RES	Ground
Blue Grouse	*Dendragapus obscurus*	RES	Ground
Killdeer	*Charadrius vociferus*	NTM	Ground
Solitary Sandpiper	*Tringa solitaria*	NTM	Tree
Great Horned Owl	*Bubo virginianus*	RES	Tree
Northern Pygmy Owl	*Glaucidium gnoma*	RES	Cavity
Boreal Owl	*Aegolius funereus*	RES	Cavity
Rufous Hummingbird	*Selasphorus rufus*	SDM	Tree
Belted Kingfisher	*Ceryle alcyon*	NTM	Burrow
Red-naped Sapsucker	*Sphyrapicus nuchalis*	SDM	Cavity
Downy Woodpecker	*Picoides pubescens*	RES	Cavity
Hairy Woodpecker	*Picoides villosus*	RES	Cavity
Three-toed Woodpecker	*Picoides tridactylus*	RES	Cavity
Black-backed Woodpecker	*Picoides arcticus*	RES	Cavity
Northern Flicker	*Colaptes auratus*	SDM	Cavity
Pileated Woodpecker	*Dryocopus pileatus*	RES	Cavity
Olive-sided Flycatcher	*Contopus cooperi*	NTM	Tree
Western Wood-Pewee	*Contopus sordidulus*	NTM	Shrub
Hammond's Flycatcher	*Empidonax hammondii*	NTM	Tree
Dusky Flycatcher	*Empidonax oberholseri*	SDM	Shrub
Pacific Slope Flycatcher (ex. Western)	*Empidonax difficilis*	SDM	Tree

continues...

Table A.1, continued…

Cassin’s Vireo (ex. Solitary)	*Vireo cassinii*	NTM	Tree
Warbling Vireo	*Vireo gilvus*	NTM	Shrub
Red-eyed Vireo	*Vireo olivaceus*	NTM	Tree
Blue Jay	*Cyanocitta cristata*	RES	Tree
Steller’s Jay	*Cyanocitta stelleri*	RES	Tree
Gray Jay	*Perisoreus canadensis*	RES	Tree
Clark’s Nutcracker	*Nucifraga columbiana*	RES	Tree
American Crow	*Corvus brachyrhynchos*	SDM	Tree
Common Raven	*Corvus corax*	RES	Tree
Black-capped Chickadee	*Poecile atricapilla*	RES	Cavity
Mountain Chickadee	*Poecile gambeli*	RES	Cavity
Red-breasted Nuthatch	*Sitta canadensis*	RES	Cavity
Brown Creeper	*Certhia americana*	RES	under bark
Winter Wren	*Troglodytes troglodytes*	SDM	cavity/stump
Golden-crowned Kinglet	*Regulus satrapa*	SDM	Tree
Ruby-crowned Kinglet	*Regulus calendula*	SDM	Tree
Mountain Bluebird	*Sialia currucoides*	SDM	Cavity
Townsend's Solitaire	*Myadestes townsendi*	SDM	Ground
Veery	*Catharus fuscescens*	NTM	Ground
Swainson's Thrush	*Catharus ustulatus*	NTM	Tree
Hermit Thrush	*Catharus guttatus*	SDM	Ground
American Robin	*Turdus migratorius*	SDM	Tree
Varied Thrush	*Ixoreus naevius*	SDM	Tree
Cedar Waxwing	*Bombycilla cedrorum*	SDM	Tree
Orange-crowned Warbler	*Vermivora celata*	NTM	Ground
Yellow-rumped Warbler	*Dendroica coronata*	SDM	Tree
Townsend's Warbler	*Dendroica townsendi*	NTM	Tree
MacGillivray's Warbler	*Oporornis tolmiei*	NTM	Shrub
Wilson's Warbler	*Wilsonia pusilla*	NTM	Ground
Western Tanager	*Piranga ludoviciana*	NTM	Tree
Chipping Sparrow	*Spizella passerina*	NTM	Tree
Brewer's Sparrow	*Spizella breweri*	SDM	Shrub
Vesper Sparrow	*Pooecetes gramineus*	SDM	Ground
Fox Sparrow	*Passerella iliaca*	SDM	Ground
Lincoln's Sparrow	*Melospiza lincolnii*	NTM	Ground
White-crowned Sparrow	*Zonotrichia leucophrys*	SDM	Ground
Dark-eyed Junco	*Junco hyemalis*	SDM	Ground
Brown-headed Cowbird	*Molothrus ater*	SDM	Parasite
Pine Grosbeak	*Pinicola enucleator*	RES	Tree
Purple Finch	*Carpodacus purpureus*	SDM	Tree
Cassin's Finch	*Carpodacus cassinii*	SDM	Tree
White-winged Crossbill	*Loxia leucoptera*	SDM	Tree
Pine Siskin	*Carduelis pinus*	SDM	Tree

APPENDIX B

OBSERVATIONAL DATA OF LARGE & MEDIUM VERTEBRATES IN THE STUDY AREA

In a long-term study of vertebrate populations in the Yukon, Hochachka et al. (2000) found that encounter rates were generally an accurate reflection of variation in population size. Thus, I thought it useful to collect encounter data on large and medium vertebrates in the study area. Although the data may not be directly pertinent to this dissertation, it provides a baseline for future comparisons in the study area, and did not involve any extra cost in collecting.

During the three years of the study, each field worker kept a record of large and medium mammals, grouse, raptors, Common Raven (scientific names in Table B.1) and snowshoe hare seen while working in the study area (Table B.1) along with the total number of hours worked (Table B.2). Workers were trained to identify all mammal and raptor species in the study area. To be included, a species had to be visually observed, not aurally detected. Observations made and time spent while travelling by vehicle were kept separately from observations made and time spent while travelling on foot or All Terrain Vehicle (ATV). This was because areas reached on foot or by ATV were generally of higher elevation than areas traversed by roads, and because differences in the mode of travel may influence what species are detected and how often they are detected. If two or more people were travelling together and all observed an animal, only one person recorded the animal, but all persons recorded their hours. All times were recorded in tenths of an hour. Data collection occurred between May 1 and August 7 of 1997 through 1999.

Only data for common species (wapiti, deer) or species of interest (grizzly and black bear) are summarized here. For monthly summaries, august sightings and hours were combined with those from July. The numbers calculated here are simply total observations per 100 hours and thus have no error associated with them, so statistics cannot be used to compare trends among years. General trends among years are evident in some cases, however, the cause of any trends cannot be identified from these data.. Differences among years within species may be due to actual population changes or differences in sightability due to different weather conditions among years.

Vehicle sighting were dominated by wapiti and deer; foot sightings by wapiti, deer and grouse (Figure B.1). Most sightings (92 %) of grouse were Ruffed Grouse or Spruce Grouse. Annual trends in sightings on foot as compared to vehicle were similar for two species (mule deer, snowshoe hare), but differed for the other five (grizzly bear, black bear, white-tailed deer, wapiti, grouse) (Figure B.1). For example, white-tailed deer sightings from vehicles peaked in 1999, but sightings on foot were similar in 1997 and 1999.

Four of the seven species peaked in 1998, including the two species that show cyclic population fluctuations in northern Canada, grouse and snowshoe hare. (Banfield 1974).

Trends in detections among months were also evident (Figures B.2 - B.4). In general, animals were detected more frequently in May and June than in July and early August. This likely relates to the movements of most bears and ungulates into higher elevation areas as the summer progresses.

Table B.1 Species recorded by observers.

Common Name	Scientific Name[1]
Grizzly Bear	*Ursus arctos*
Black Bear	*Ursus americanus*
Coyote	*Canis latrans*
White-tailed Deer	*Odocoileus virginianus*
Mule Deer	*Odocoilus hemionus hemionus*
Wapiti	*Cervus elaphus*
Moose	*Alces alces*
Bighorn Sheep	*Ovis canadensis canadensis*
Mountain Goat	*Oreamnos americanus*
Pine Marten	*Martes americana*
Porcupine	*Erithizon dorsatum*
Snowshoe Hare	*Lepus americanus*
Spruce Grouse	*Falcipennis canadensis franklinii*
Ruffed Grouse	*Bonasa umbellus*
Blue Grouse	*Dendragapus obscurus*
Northern Goshawk	*Accipiter gentilis*
Red-tailed Hawk	*Buteo jamaicensis*
Bald Eagle	*Haliaeetus leucocephalus*
Common Raven	*Corvus corax*

[1] after BC Ministry of Sustainable Resource Management (2001)

Table B.2 Total number of observers and person-hours worked in the study area.

	1997	1998	1999
# observers	4	6	6
Total person hours –foot	814.5	1020.5	1565.8
Total person hours - vehicle	337.5	385.2	599.8
Total person hours	1152	1405.7	2165.6

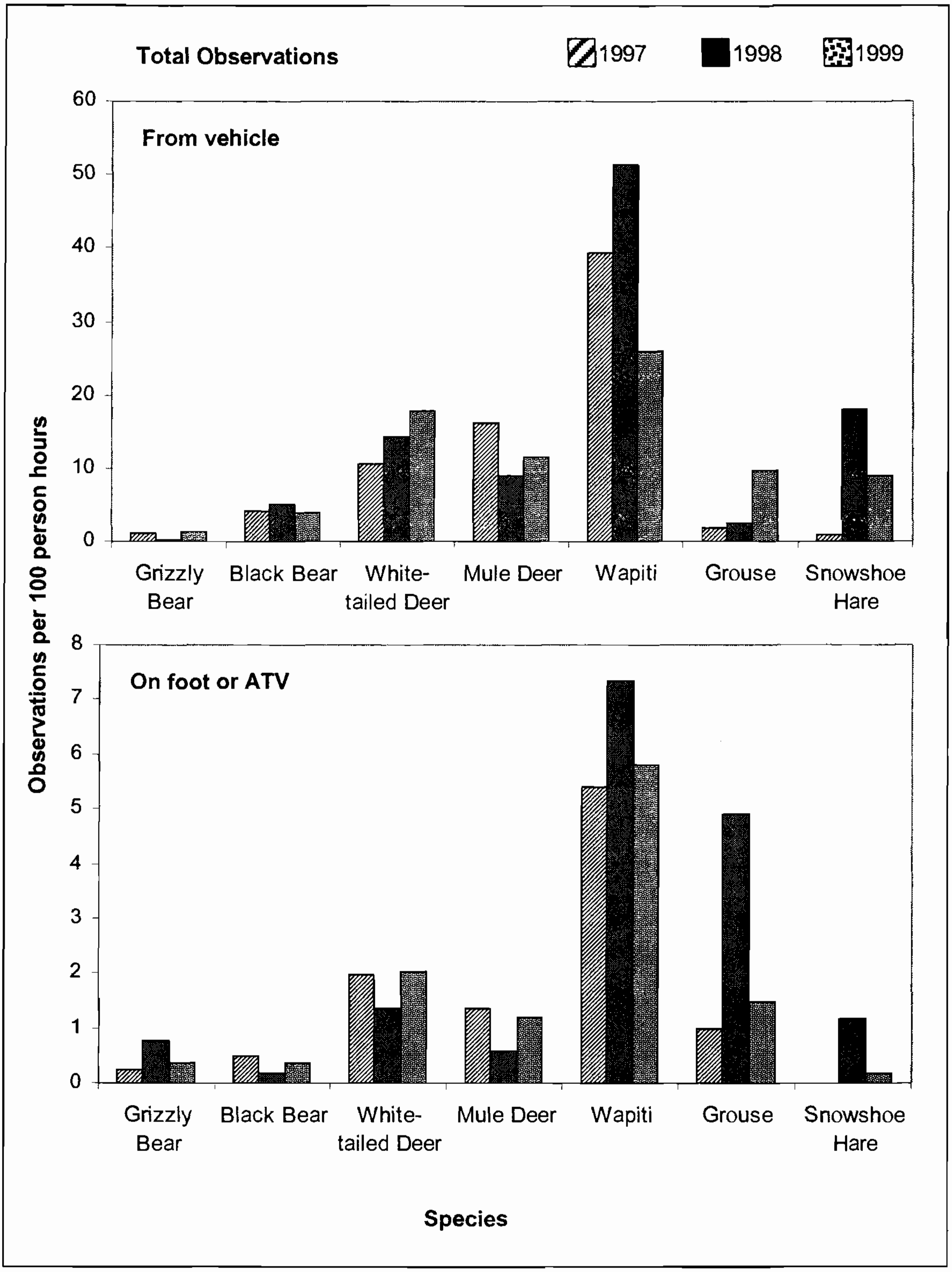

Figure B.1 Total annual observations of Grizzly Bear, Black Bear, White-tailed Deer, Mule Deer, Wapiti, Grouse and Snowshoe Hare per 100 person hours, from vehicles and on foot or All-Terrain Vehicle (ATV), in 1997, 1998 and 1999. Note large difference in Y-axis.

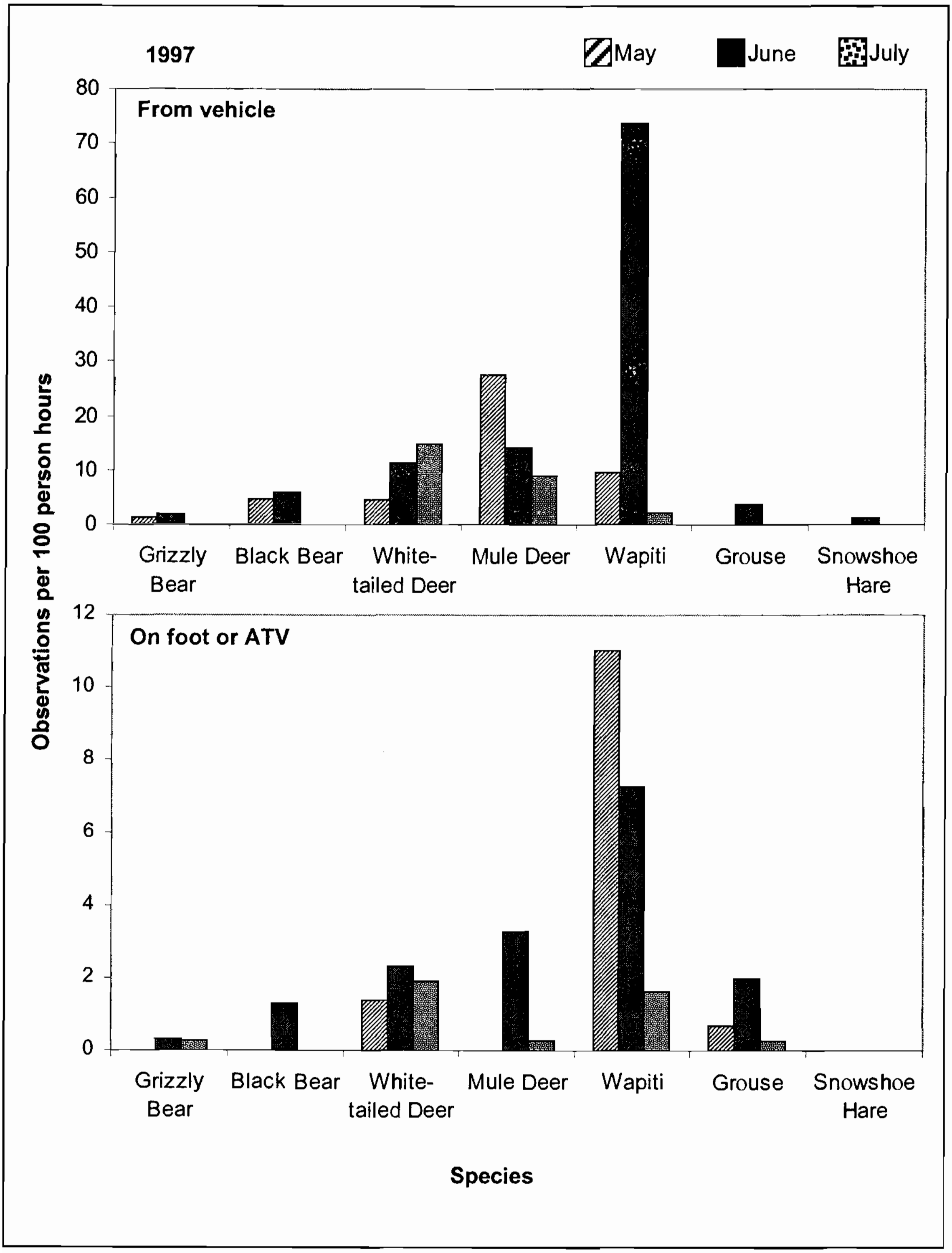

Figure B.2 Observations in 1997of Grizzly Bear, Black Bear, White-tailed Deer, Mule Deer, Wapiti, Grouse and Snowshoe Hare per 100 person hours, from vehicles and on foot or All-Terrain Vehicle (ATV), in May, June and July. Note large difference in Y-axis.

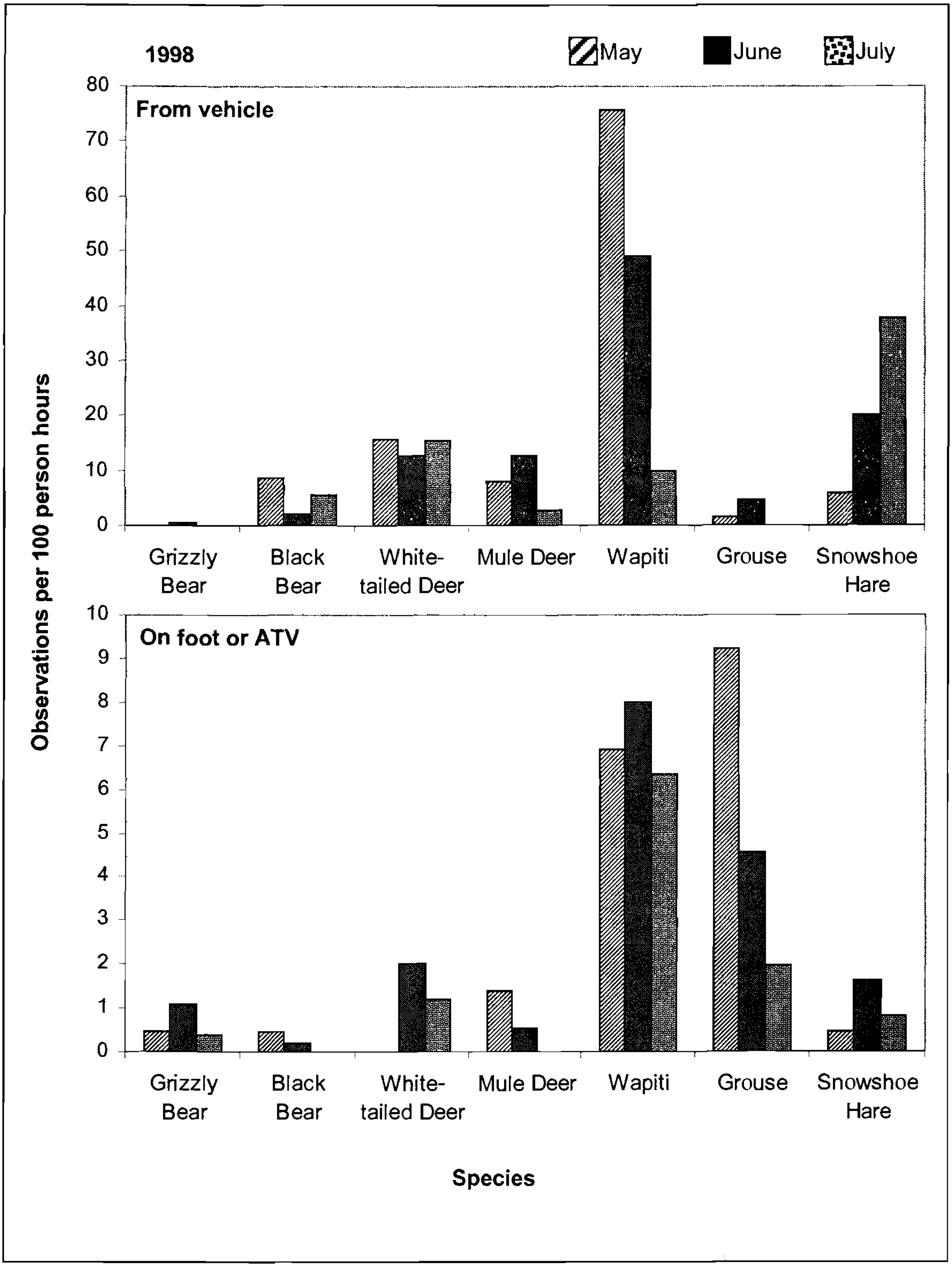

Figure B.3 Observations in 1998 of Grizzly Bear, Black Bear, White-tailed Deer, Mule Deer, Wapiti, Grouse and Snowshoe Hare per 100 person hours, from vehicles and on foot or All-Terrain Vehicle (ATV), in May, June and July. Note large difference in Y-axis.

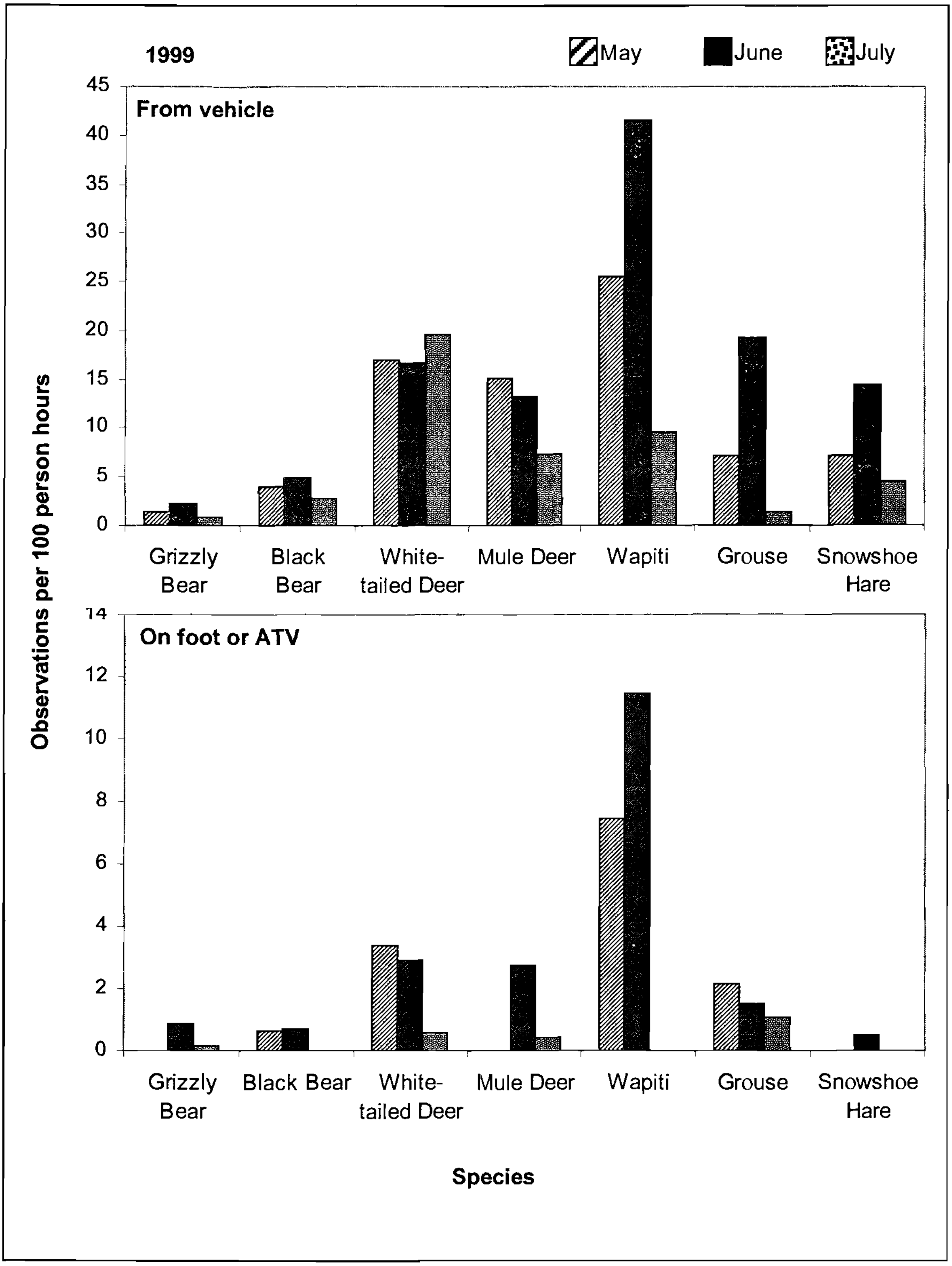

Figure B.4 Observations in 1999 of Grizzly Bear, Black Bear, White-tailed Deer, Mule Deer, Wapiti, Grouse and Snowshoe Hare per 100 person hours, from vehicles and on foot or All-Terrain Vehicle (ATV), in May, June and July. Note large difference in Y-axis.

APPENDIX C

RESULTS FROM RED SQUIRREL AND GRAY JAY HYPOTHESIS TESTS.

To determine if the abundance of red squirrel (*Tamiasciurus hudsonicus*) or Gray Jay (*Perisoreus canadensis*) was influenced by disturbance type or residual trees, regression analysis was conducted as per the analysis in Chapter 2. Data on red squirrels and Gray Jays were collected through point counts, as for the songbirds. The mean abundance of the species was the dependent variable, disturbance type, density of residual conifer overstory trees, and density of residual conifer understory trees were used as independent variables, and stand age and elevation were used as co-variates. For both species a detection radius of 130 m was used. For full details on the analysis, see Chapter 2 *Methods*. Stepwise multiple linear regression was used for the red squirrel data since it met the assumptions for this method. Stepwise logistic regression was conducted on the Gray Jay data rather than Poisson regression, because Gray Jays were detected in less than half the stands. To increase sample size, the Montane Spruce (MS) and the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zones were combined for analysis. The drop in deviance test was used to assess variable significance.

Detections of red squirrels were higher in logged than burned stands in the Montane Spruce (MS) biogeoclimatic subzone (Table C.1). In the MS red squirrels increased in abundance with logging, stand age and residual overstory conifer trees, but decreased with increasing elevation and densities of residual understory conifers (Table C.2). In the ESSF, red squirrels increased in abundance with stand age (Table C.2) and were higher in logged than burned stands, after accounting for the effect of stand age (Table C.1, C.2).

The probability of Gray Jays being present in a stand increased with increasing densities of residual overstory conifer trees, but no effects of elevation, age, disturbance type, or understory conifer trees were detected (Table C.2). The mean abundance of Gray Jay was similar in logged and burned stands in the MS and the ESSF (Table C.1).

Table C.1 Mean abundance (± SE) of Red Squirrel and Gray Jay at the 174 point count stations in the study area, based on three surveys per year for three years at each station.

	MS		ESSF	
	Burn (n=23)	**Log** (n=79)	**Burn** (n=45)	**Log** (n=27)
Red Squirrel	0.61 ± 0.9	0.81 ± 0.6	0.38 ± 0.07	0.38 ± 0.06
Gray Jay	0.10 ± 0.03	0.12 ± 0.02	0.08 ± 0.02	0.08 ± 0.02

Table C.2 Results of the model runs for red squirrel and Gray Jay, in each biogeoclimatic ecological classification (BEC) zone. Only variables that were significant in the models are listed.

	BEC Zone	**Significant Variables**	**Estimate ± SE**	**p**
Red Squirrel	MS†	Elevation	-0.001 ± 0.004	0.0001
		Age	0.04 ± 0.006	0.0001
		Disturbance Type	0.64 ± 0.16	0.0068
		Overstory Conifers	0.28 ± 0.05	0.0001
		Understory Conifers	-0.17 ± 0.04	0.002
	ESSF	Age	0.03 ± 0.009	0.004
		Disturbance Type	0.36 ± 0.20	0.07
Gray Jay	MS & ESSF‡	Overstory Conifers	0.20 ± 0.09	0.03

† Multiple linear regression, model r^2= 0.61 for MS, r^2= 0.19 for ESSF.

‡ Logistic Regression