

**BOREAL FOREST SONGBIRD DIVERSITY AND REPRODUCTIVE
SUCCESS: ROLES OF VEGETATION, PREDATORS,
AND COMPETITORS**

A Thesis

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Doctor of Philosophy in the Department of Biology.
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By

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ABSTRACT

The hypothesis that predators diversify songbird communities, by preying more heavily on individuals and species with greatest similarity in nest-site use, was evaluated using field studies in boreal forests of Alberta and Saskatchewan and artificial nest experiments in Alberta. Positive relationships between predator diversity or abundance and diversity of birds were detected, after controlling effects of vegetation. There were more positive and non-significant than negative associations between ecologically similar congeners, suggesting only limited effects of competition on bird diversity. Predator responses to artificial songbird nests that varied in placement, vegetation features and dispersion patterns were also examined. Predators were expected to destroy nests characterized by similar vegetation features or nest types. Variability among nest sites was achieved by deploying nests throughout a gradient of vegetation and by deploying nests to simulate two- and three-species assemblages. However, predation did not increase as variance in vegetation surrounding nest sites decreased across plots; nor did variance in vegetation surrounding successful nests increase among plots as predation increased. The addition of another species' nest type to assemblages did not result in lower predation rates, nor did predators destroy more clumped than randomly distributed nests. Data from these and other artificial nest experiments were used to identify habitat attributes associated with successful nests versus those destroyed by specific predators. Successful nests and those visited by mice tended to be ground nests well-concealed by dense shrubs. Squirrels and birds usually visited above-ground nests at sites with few shrubs and high tree densities.

Reliability of methods used to obtain patterns of songbird productivity was tested using artificial nests (visual and olfactory cues) and indices of reproductive success in mixedwood forest of Alberta. Avian predators did not discriminate between wicker nests dipped in mud and wicker nests covered by a camouflage fabric, whereas mammalian predators showed a weak tendency to depredate camouflaged nests. Nests containing plasticine eggs in field experiments and egg assortments containing plasticine eggs in laboratory experiments with captive deer mice (*Peromyscus maniculatus*) were depredated more than those only containing finch and quail eggs. Young and old forest

stands were used to compare differences in reproductive effort and success, using songbird behavior and number of fledglings. Some species differed in density (17%), indices of reproductive behavior (33%), and number of fledglings observed (13%) between stand-ages. Using behavioral indices or fledgling numbers to estimate nesting success in forested habitats did not appear feasible due to visibility biases, low statistical power, and an inability to verify the index using natural nests. Also, a presumed positive relationship between indices of reproductive success and density were obtained for only 40–45% of species.

Overall, results were consistent, in part, with evidence that mechanisms other than competition or vegetation structure may contribute to forest songbird community structure. My findings also suggest that predators diversify songbird communities, though discrepancies exist between results from natural songbird communities versus artificial nests possibly because artificial nests do not portray reliable predation events. Further experimental research is required to clarify the role predators play in structuring songbird communities and to refine methodology used to detect patterns of avian reproductive success.

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...three family members with hearts of gold whose lives exemplified generosity, compassion, and self-sacrifice. Their love of simple pleasures and devotion to family remain beacons across the years.

Ability is what you're capable of doing.

Motivation determines what you do.

Attitude determines how well you do it.

-Lou Holtz

Many, many, many people.....

-Zola Littlechild

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1. GENERAL INTRODUCTION

Identifying patterns of natural assemblages of birds and understanding the processes underlying these patterns has been a primary focus of community ecology since the 1950s. Avian community patterns are consequences of the species composition of the community, the distribution, abundance, and morphological and behavioral attributes of those species, and the ways these relate to the environment (Wiens 1989a). A primary metric of community patterns is species diversity derived from the number of species and the abundance of individual species. Communities can also be structured into clusters of species of similar ecology or ecological guilds, such as nesting guilds. Consideration of guilds may reveal community patterns that are masked by the detail of species-specific analyses (Wiens 1989a).

Identifying patterns of ecological separation among species is generally based on resource use, where resources are critical features used by birds that are potentially limiting (e.g., food, space, nest sites, mates, singing perches; Schoener 1974, Cody 1985). Habitat is not considered a specific resource, rather it reflects the spatial distribution and accessibility of resources. Choice of nesting locations has typically received much less attention than food or habitat parameters in studies of resource partitioning, particularly for open-cup nesting species, possibly because nest sites are presumed to be unlimited (Wiens 1989a).

Population and community patterns provide the foundation for hypotheses related to vegetation structure, competition, predation, history, phylogeny, fluctuating resources levels, physiological capabilities, or other features of the species and their environment. Historically, studies have argued about the singular importance of competing hypotheses to explain avian community structure (Nudds 1983). For example, the search for patterns in bird communities has usually been conducted within the framework of the “MacArthurian” paradigm, which focuses on interspecific competition as the major

process determining these patterns (Wiens 1989a). Classical competition theory argues that species will differ in some basic ways, as ecologically identical species cannot coexist (Schoener 1974). Yet, there are clearly several factors besides competition that, until recently, had not been examined as potentially influencing community characteristics. Furthermore, recent attention has focused on the relative importance and interactive nature of ecological processes structuring avian communities (Brown 1988, Telleria *et al.* 1992).

One of the most thoroughly documented patterns is the positive association between avian diversity and measures of habitat complexity, a relationship that is consistent across biogeographic regions (Terborgh 1977). The role that vegetation structure plays in bird species diversity was advanced almost four decades ago with the work of the MacArthurs (MacArthur and MacArthur 1961, MacArthur *et al.* 1962). They showed that foliage height diversity, an index of vegetation structural heterogeneity, predicted bird species richness and diversity. Considerable evidence confirms that vegetation is a primary driving force organizing songbird communities, with structural components of vegetation providing strong predictors of bird community abundance and composition (Karr and Roth 1971, Røv 1975, Terborgh 1977, Schieck *et al.* 1995, Kirk *et al.* 1996). Though much work has focused on establishing empirical relations between habitat structure and bird diversity, causal mechanisms remain unclear. Additional hypotheses may account for variation in songbird communities after vegetation is accounted for, and these may also help to explain associations between habitat and avian communities.

Predation is one alternative hypothesis that has been advanced to explain variation in avian community diversity, yet there have been remarkably few tests of Martin's ideas (Martin 1988a, 1993a). The central premise is that predation pressure varies among species, habitats, and geographical areas, modifying life-history traits, habitat selection, and subsequently, population and community patterns (Slagsvold 1982, Martin 1987a). More specifically, assuming that predation is density-dependent, predation can act as an evolutionary process that selects for a more diverse avian community, hereafter termed the predation hypothesis (Martin 1988b). When different songbird species use the same site for nesting, they may be at a higher risk of predation if predators respond to several species as though they were one, based on nest type or

location. Any subsequent nest-site partitioning by coexisting species that reduces predation risk may result in a more diverse bird community. A greater variety of nest types and locations may force predators to search more substrates and heights decreasing predator searching efficiency, inhibiting the development of predator search images and, ultimately, lowering nest predation (Martin 1988b, 1993a). Because very few natural and manipulative experiments have been conducted to address the predation hypothesis, in Chapter 2, I examined relationships between predator diversity and bird diversity in boreal forest of Alberta and Saskatchewan. In Chapter 3, I continued to evaluate the importance of predators in structuring songbird communities and influencing nest dispersion patterns by using experiments with artificial nests.

Predators are the principal cause of nesting mortality in birds and may influence patterns of nest-site selection (Ricklefs 1969). Traditional studies of nest placement compared vegetation attributes and nesting success among nest sites and random sites, nest patches, territories and coexisting species to understand factors that potentially affect avian habitat selection and, ultimately, factors that are involved in structuring avian communities (Rice 1983, Martin and Roper 1988, Bergin 1992, Kelly 1993, Braden *et al.* 1997). A novel approach is to identify nest vegetation variables that are associated with specific groups of nest predators, thereby examining predation by different predators relative to specific locations of nests (Chapter 4). This approach is valuable because nest predation risk is generally not the same for nests placed on the ground, in shrubs, or in trees (Martin 1993b, Hannon and Cotterill 1998). The type of nest predator associated with nest locations, the predation risk these predators represent, and the ability of individuals of different bird species to cope with different predators are assumed to be factors affecting avian community patterns.

Due to difficulty in directly examining pattern and process related to predation, investigators commonly employ artificial nests to provide insight into apparent differences in predation rates among areas or species (Martin 1988b, Sieving and Willson 1998). However, predators may not always respond to artificial nests in the same way they do natural nests (Martin 1987a, Willebrand and Marcström 1988, Major and Kendal 1994). Artificial nests and their contents may either attract or repel predators due to unnatural

odors and appearances (Møller 1987, Martin 1987a, Götmark 1992a, Whelan *et al.* 1994, Bayne and Hobson 1999). Consequently, if artificial nests are to be used as a tool to reveal and test hypotheses about songbird community patterns, potential biases associated with this approach should be critically assessed. By combining both field and laboratory experiments (Chapter 5), I addressed issues of artificial nest appearance and olfactory cues emitted by different egg types. Specifically, predator responses to wicker nests dipped in mud and wicker nests covered in a camouflage fabric were compared as were predator responses to nests containing quail and finch eggs versus quail, finch, and plasticine eggs. Laboratory experiments focused on choice of egg type by deer mice (*Peromyscus maniculatus*), which are considered key predators of eggs of ground-nesting songbirds (Bayne *et al.* 1997).

An understanding of pattern and process for avian communities is essential for effective conservation of songbirds. Patterns of abundance or habitat use are generally relied upon to develop and implement management initiatives. This approach can be problematic for two reasons. Firstly, abundance or density is frequently used as a good indicator of habitat quality, despite evidence that these measures are not consistent predictors of habitat quality (Van Horne 1983, Vickery *et al.* 1992a, Roberts and Norment 1999). Secondly, predictive relationships between habitat features and density are only useful under the same environmental conditions, and these relationships provide no insight into processes affecting the reproductive behavior of birds (Rotenberry 1986). Habitat characteristics, as well as ecological processes like competition and predation, influence fitness by affecting the quantity and dispersion of foraging and nesting patches, and subsequently, recruitment and community patterns. Consequently, measures of reproductive success are critical to facilitate an understanding of basic breeding biology, habitat selection, and population demography for both evolutionary and managerial perspectives (Martin 1992). Because direct measures of productivity (e.g., clutch size, nestling growth rates, fledgling weight) can be logistically difficult to obtain, researchers have used indirect measures (e.g., pairing success, behavioral observations; DeSante and Geupel 1987, Martin and Geupel 1993, Ralph *et al.* 1993). For instance, reproductive behaviors, such as apparently mated

pairs, carrying food, and carrying fecal sacs, have been used successfully in grassland habitats to estimate relative productivity and to develop reproductive behavior indices (Vickery *et al.* 1992a, Hartley 1994, Dale *et al.* 1997). Because the reliability of this technique, to my knowledge, was untested in boreal forest, I examined the ease of detecting reproductive behaviors in young and old boreal forest and related the number of reproductive behaviors to bird density to evaluate the presumed predicted positive relationship between productivity and a measure of habitat use (Chapter 6). The thesis concludes (Chapter 7) with an overall synthesis of major findings and recommendations for future work.

2. FOREST BIRD COMMUNITY STRUCTURE: ROLES OF VEGETATION, PREDATORS, AND INTERSPECIFIC COMPETITION

2.1 INTRODUCTION

Factors proposed to explain avian community patterns of species abundance and composition include competition for food and nest sites, predation, brood parasitism, climate, and habitat features (MacArthur and MacArthur 1961, Cody 1974, Holmes and Schultz 1988; Martin 1988a, 1993a; Willson and Comet 1996a, Grzybowski and Pease 1999). Debate in the late 1970s and early 1980s concentrated on the role of food-based competition as the central ecological process shaping avian communities (Schoener 1974, Diamond 1978, Connell 1983). Although the role of predation was advanced as an alternative to competition for resource partitioning and resulting community organization (Connell 1975, Wiens 1977, Strong *et al.* 1983), the hypothesis that predators of birds may be a strong selective force shaping avian species coexistence was not rigorously tested until the late 1980s. It is now well established that vertebrate predators affect community structure in aquatic systems (Sih *et al.* 1985, Hanazato and Yasuno 1989); and, Martin (1988a,b,c, 1993a, 1996) provided convincing evidence that predation should also be considered as a process shaping avian communities. Not only do predators account for the largest proportion of nest losses (Ricklefs 1969, Martin 1992), but it has been demonstrated recently that predation and risk of predation influence the evolution of life-history traits and behavioral decisions of birds (Suhonen *et al.* 1994, Martin 1995, Bosque and Bosque 1995, Norrdahl and Korpimäki 1998). Nonetheless, since Martin's first paper on this topic in 1988, remarkably few researchers have followed his lead to test the importance of predation in determining breeding bird assemblages. Here, I evaluate critically research in this area and also provide a test of the role of predators in bird community organization.

Martin (1988a,b,c, 1993a) postulated that nest-site partitioning among coexisting

species results from combined effects of density-dependent predation on eggs and nestlings and predator specialization on nest types. This occurs by predators responding to accumulating densities of similar nesting songbird species as though they were one species. As numbers of similar species increase in abundance, each species experiences a greater rate of nest predation. Predation imposes a selective pressure for coexisting species to select different nest types and locations, thereby decreasing the searching efficiency of predators. This hypothesis, hereafter termed the predation hypothesis, predicts that the degree of similarity of nest sites among coexisting species will diverge over evolutionary time as a direct consequence of selective predation. Moreover, empirical studies have focused largely on predator responses to artificial nests (Martin 1988b, Marini 1997, Sieving and Willson 1998) rather than natural nests in relatively simple environments (Martin 1993a, 1996); thus, it remains unclear whether such findings extend to songbirds and predators in spatially and temporally complex habitats and landscapes.

Hypotheses to explain avian community structure are not mutually exclusive because ecological factors may interact, making interpretation of observed patterns difficult. Furthermore, several underlying mechanisms that may explain avian community structure make common predictions. For example, just as predators may provide selective pressure to increase bird diversity so may increased vegetation complexity (MacArthur and MacArthur 1961, Røv 1975, Terborgh 1977). Interspecific competition theory predicts that species will coexist and, hence, increase avian diversity, if foraging space is partitioned such that competition is reduced (Schoener 1974). Also, local climates with high ambient temperatures may give rise to more diverse bird communities, potentially through proximate causes such as increased insect abundance or broader physiological tolerance (Sabo and Holmes 1983). Consequently, the strength of the predation hypothesis in explaining assemblages of avian communities is best assessed by either controlling or manipulating additional contributory factors or simultaneously testing alternative hypotheses to ascertain their relative importance.

I first reviewed studies published during the past decade to evaluate which alternative hypotheses were investigated and outcomes of those investigations regarding

the organization of avian communities. In a field study, I then tested for evidence of predators acting as a selective pressure on birds in boreal forests of Alberta and Saskatchewan. Following Martin (1988a,b), I predict that predator diversity or individual predator abundance will be positively correlated with bird diversity, after controlling for effects of variation in vegetation composition and structure. To assess whether competition may also be operating to structure forest bird communities, I examined whether abundances of pairs of congeners within the same foraging guild were negatively correlated, while controlling for vegetation effects and predator abundance.

2.2 METHODS

2.2.1 Literature Review

To determine whether community ecology has progressed in evaluating predation as a process organizing avian communities in the past decade, a survey was made of all articles in *Auk*, *Bioscience*, *Canadian Journal of Zoology*, *Condor*, *Ecology*, *Ecological Monographs*, *Evolutionary Ecology*, *Oecologia*, *Oikos*, *Nature*, *Proceedings of the National Academy of Science*, and *Science* (1988 to 1998). This was not meant to be an exhaustive literature review as undoubtedly relevant articles exist in other journals, but rather a method for presenting relative numbers of different types of articles evaluating factors affecting avian communities primarily in North America. Journals were chosen for this survey because they were primary bird ecology journals, reported tests of ecological factors affecting avian community structure, or included studies that specifically evaluated the predation hypothesis. Most studies conducted either field experiments or computer modeling. No single-species studies, reviews, or comments were included in the review. I classified articles according to the type of ecological factor(s) used to evaluate avian community structure (i.e., habitat, interspecific competition, predation, food, weather, brood parasitism) and whether these factors had positive, negative, or non-significant effects. Even though competition traditionally refers to reciprocal negative effects (Wiens 1989a), I also included all studies involving asymmetrical situations where only one member of a pair of species was negatively

affected. I recorded if the predation hypothesis was tested specifically, if artificial nests were used, and the number of bird species examined in each study. Articles that examined more than one ecological factor were counted as one study per factor. Articles were tabulated based on whether they tested single or multiple factors. Multi-factor studies were further separated by whether additional factors were controlled while individual factors were tested or whether additional factors were not controlled. I used Spearman rank correlation to determine whether studies of the predation hypothesis had become relatively more common over the past decade.

2.2.2 Field Study

One study area in Alberta and one in Saskatchewan were selected to examine the relationship between predator diversity/abundance and songbird diversity in boreal forest, where little is known about predator-prey dynamics. Because study areas were in separate geographical locations but still within the same boreal forest ecozone, two independent tests of the predation hypothesis were conducted. Point-counts were used to measure relative bird and predator (i.e., jay and red squirrel) abundance (see below for details). Vegetation attributes were estimated at point-count stations to control for additional effects of habitat structure and composition on bird diversity. Data within geographical areas were collected in multiple years with different timing of point-count surveys within seasons and different vegetation sampling methods. This was because these data were collected as part of a larger study that examined other ecological questions. Nonetheless, all animal abundance estimates were collected by standard point-counts, and well established sampling techniques for forest vegetation were used. To test the predation hypothesis, I needed a range of variation in bird and predator diversity. Because avian and predator diversity vary with cover type and age-class of forest (Rusch and Reeder 1978, Kirk *et al.* 1996), it was necessary to pool data across years to attain the fullest possible range of natural variation in diversity (e.g., in 1991, sites in Alberta were only in old stands of white spruce (*Picea glauca*) and these were combined with other site-types in other years).

2.2.2.1 Foothills Natural Region of Alberta

Study sites were located within a 70 km radius of Hinton, Alberta (53°24'N, 117°35'W), in the (Boreal) Lower and Upper Foothills Natural Regions (Beckingham *et al.* 1996a). Codominant tree species in the Lower Foothills (500 to 1150 m) include trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), lodgepole pine (*Pinus contorta*), and white spruce. The Upper Foothills (900 to 1500 m) is dominated by closed-canopy coniferous forests, primarily lodgepole pine. Data from the Alberta natural regions were collected as part of a doctoral dissertation at the University of Alberta (Farr 1995). Data were collected from 1990 to 1992 and I assisted in data collection only in 1992.

Birds, red squirrels (*Tamiasciurus husonicus*), and tree and shrub cover attributes were recorded at 98 sites of unlogged forest of fire origin ($n = 65$) or forest of post-logging origin ($n = 33$) over a three year period (1990 to 1992). Twenty-seven sites with a history of logging contained patches of uncut or residual forest. Sites were located ≥ 1 km apart and encompassed an array of forest cover types and age-classes (Table 2.1; see Appendix A for representative forest stand diagrams). Previously logged stands that contained residual trees have stand-ages reported for both logged and residual patches. In 1990, there were 17 sites each containing five point-count stations 300 m apart, except for two sites containing one station each and a third containing six stations. In 1991, there were nine sites each containing 12 point-count stations separated by 300 m. In 1992, there were 72 sites each containing 10 stations 400 m apart. All stations were ≥ 200 m from forest edges.

Relative bird and red squirrel abundance were sampled using the variable-radius point-count method (Reynolds *et al.* 1980). In 1990, sites were visited between late May and early July and in 1991 and 1992 sites were visited in June. Sampling began one half-hour before sunrise (about 0500 MST) and ended within four hours. At each station, all auditory and visual observations made in a 10-minute period were recorded. So that animals were only included in the area sampled for vegetation, observations estimated to be >150 m away from stations were excluded. In 1990, sites were sampled between one and four times by two observers. One of these observers sampled all sites

Table 2.1. Description of forest stands from Alberta (1990 to 1992) and Saskatchewan (1994 to 1995).

Cover type	Age-class	Age (years)	Residual present ^a	Residual age (years)	Number of stands
Alberta					
Deciduous	young	13	Y	41	1
Deciduous	mature	95	N		1
Deciduous	old	105+	N		2
Mixedwood	young	22-33	Y	28-47	14
Mixedwood	mature	95	N		3
Mixedwood	old	105+	N		11
Lodgepole pine	young	18-23	Y	32-49	4
Lodgepole pine	old	107	N		6
Black spruce	mature	99	N		1
Black spruce	old	106+	N		4
White spruce	old	105+	N		3
Spruce-fir	young	21-30	Y	39	4
Spruce-fir	mature	71	N		1
Spruce-fir	old	128+	N		9
Spruce-pine	young	15-33	Y	39-47	10
Spruce-pine	mature	94-95	N		2
Spruce-pine	old	103+	N		22
Saskatchewan					
Aspen	young	15-25	N		4
Aspen	old	100+	N		1
Mixedwood	mature	55-85	N		4
Mixedwood	old	100+	N		9
Jack pine	young	15-25	N		6
Jack pine	mature	50-80	N		3
Jack pine	old	100+	N		11
Black spruce	old	100+	N		7
White spruce	old	100+	N		6
Black spruce-white spruce	old	100+	N		1
Larch	old	100+	N		2
Jack pine-black spruce	old	100+	N		6

^a Y = yes and N = no for stands of logging origin containing patches of uncut residual trees.

twice in 1991. In 1992, six additional observers sampled 12 sites once each, with dominant forest cover types distributed evenly among observers. When stations were visited more than once, the visit with the maximum number of individuals per species was analyzed because frequency of detection may vary within and among species during the course of the breeding season (Mayfield 1981, Skirvin 1981).

Vegetation sampling was conducted immediately after collection of point-count data. In 1990, vegetation attributes of sites were recorded at stations. In 1991 and 1992, some vegetation attributes for sites, as noted below, were obtained for an area of 7.1 ha (150 m radius circle) around the station. Because this area frequently contained more than one cover type, most values were the mean of all vegetation polygons weighted by the relative area of each polygon around stations. Polygons were areas defined by forest inventories based on cover type and age-class. Stand-age of unlogged and post-logging forest was obtained from fire and silvicultural history inventories, respectively. Tree height in unlogged forest was measured using a clinometer (1990 to 1991, $n = 160$ point-count stations) or obtained from digital forest cover inventories (1992, $n = 530$ stations). In post-logging forest, tree height was estimated visually (1990 to 1992, $n = 216$ stations). At all stations, tree height was the height of dominant and codominant trees in stands (Alberta Forestry, Lands and Wildlife 1991). Tree crown closure, the percent of ground covered by the vertical projection of dominant and codominant tree crowns (Alberta Forestry, Lands and Wildlife 1991), was estimated visually for unlogged (1990 to 1991, $n = 160$ stations) and post-logging forest (1990 to 1992, $n = 216$ stations) and obtained from digital forest cover inventories for unlogged forest (1992, $n = 530$ stations). The contribution of each tree species to crown closure was estimated to the nearest 10%, using the design described for shrub height (see below). In 1990, density of snags was obtained by counting the number of standing snags within a 100 m x 20 m belt transect through stations. In 1991, snags were counted in 10 x 10 m plots in each cover type polygon within 150 m of the station. In 1992, snags, in four diameter-at-breast-height (dbh) classes (tiny = 10-14.9 cm, small = 15-24.9 cm, medium = 25-34.9 cm, large = ≥ 35 cm) and over 2 m tall, were counted within a 11.3-m radius circle around stations. Shrub height and crown closure were estimated to the nearest

meter and 10%, respectively, using the design described for standing dead trees, for unlogged sites in 1990 to 1992 and post-logging sites in 1990 to 1991. Post-logging sites in 1992 ($n=190$ stations) used area-weighted means for estimates of shrub height and crown closure. Observer differences within years for both point-counts and vegetation sampling were calibrated by conducting independent auditory and/or visual estimates and comparing these until similar numbers were obtained consistently.

2.2.2.2 *Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan*

Study sites were located in contiguous forest of the Mid-Boreal and Churchill River Upland Ecoregions of Saskatchewan (Beckingham *et al.* 1996) about 70 km north of Prince Albert (53°50'N, 105°50'W) and 70 km northeast of La Ronge (55°18'N, 105°50'W). Bird and vegetation data were provided by K. A. Hobson from the Boreal Forest Bird Program of the Prairie and Northern Wildlife Research Center, Canadian Wildlife Service. In 1994, there were 40 sites, each containing four to six point-count stations ≥ 250 m apart. In 1995, there were 20 sites, each containing three to 11 point-counts stations ≥ 200 m apart. All stations were ≥ 100 m from forest edges. Stands included a range of cover types and ages (Table 2.1). All sites were of fire origin except for four young aspen sites that were examined post-logging.

Point-counts were conducted twice in June (0400 to 0900 CST) at each station to survey breeding birds and red squirrels (Blondel *et al.* 1970). At each station, all birds heard or seen during a 10-minute period were recorded. Only birds estimated to be within the stands were included in counts. Surveys were performed by two observers in 1994; one of these observers and one other performed surveys in 1995. As with the Alberta data set, the maximum number of individuals per species from multiple visits was analyzed for each station. As with the Alberta data set, observer bias was controlled through calibration.

At each point-count station, visual estimates of stand structural attributes within a 50-m radius circle were recorded. Six observers in 1994 and two observers in 1995 recorded vegetation characteristics. Attributes included estimates of the average canopy height and the percent contribution to the canopy (≥ 10 m), subcanopy (≥ 5 m and < 10 m), and shrub layer (< 5 m) of major tree and shrub species.

2.2.3 Statistical Analyses

To evaluate the relationship between bird and predator diversity, diversities were calculated at each site using the Shannon-Wiener index (Magurran 1988). Red squirrels, gray jays (*Perisoreus canadensis*), and blue jays (*Cyanocitta cristata*) contributed to measures of predator diversity. Common ravens (*Corvus corax*) and American crows (*Corvus brachyrhynchos*) were only detected flying over sites and therefore were not included as resident predators. Common names, scientific names, nesting locations, and foraging guilds of all bird species detected on sites that were considered susceptible to predation by squirrels and jays are given in Appendix B.

Because predators may discriminate among types of nesting locations more easily than individual bird species, a Shannon-Wiener diversity index was also calculated for breeding birds weighted by nest location. This was achieved by first assigning each bird species to a nesting location based on nesting sites located on my study areas (unpublished data) and Ehrlich *et al.* (1988). Nesting locations included coniferous tree, deciduous tree, shrub, ground, cavity, and vegetation above water. Species that commonly used more than one of these nest locations had an equal number of individuals assigned to each location. To weight each species by nesting location, the total number of individuals of a single species (t_a where a = one species) was multiplied by the ratio of the total number of species in a specific nest location at a site (t_{a-f} where $a - f$ = several species within the same nesting location) to the total number of species in all nest locations (t_{a-z} where $a - z$ = all species within all nesting locations; $t_a * \{t_{a-f} / t_{a-z}\}$). This weighting technique permitted the proportional abundance value in the Shannon-Wiener calculations to still equal 1.0. In addition, the diversity of ground-nesting species was analyzed separately. This enabled me to compare results of indirect tests of the predation hypothesis using observational data from natural songbird communities versus those using artificial nest data in Chapter 3.

Forward-stepwise multiple regression was used to obtain vegetation predictors that accounted for most variation in bird diversity (Zar 1984). For Alberta, diversity and weighted bird diversity were regressed on the linear combination of tree crown closure, tree height, percent of white spruce, black spruce (*P. mariana*), fir (*Abies* spp.),

lodgepole pine, larch (*Larix laricina*), trembling aspen, balsam poplar, and paper birch (*Betula papyrifera*) contributing to the canopy, percent of green alder (*Alnus crispa*) and willow (*Salix* spp.) contributing to the shrub layer, and density of tiny, small, medium, and large snags. Similarly, forward-stepwise multiple regression was used to regress bird diversity and weighted bird diversity in Saskatchewan on the linear combination of tree height, white spruce in the canopy, subcanopy, and shrub layer (%), black spruce in the canopy and subcanopy (%), fir species in the subcanopy (%), jack pine in the canopy and subcanopy (%), trembling aspen in the canopy, subcanopy, and shrub layer (%), paper birch in the canopy and subcanopy (%), *Rosa* species (%), and *Alnus* species (%). Vegetation variables were arcsine square root, log, or square root transformed to improve normality. For all linear regressions in this chapter, residuals were examined for nonlinear relationships and tests of curvilinearity were conducted (quadratic and cubic models were used where appropriate). Residuals of bird diversity and weighted bird diversity were then used as continuous response variables in simple linear regressions on untransformed or square root transformed predator diversity.

Simple linear regressions for unweighted and weighted bird and predator diversities were conducted using sites (i.e., $n = 98$ for Alberta, $n = 60$ for Saskatchewan) rather than stations to obtain greater spatial independence among replicates. This prevented inflating error degrees of freedom, but also removed the preponderance of zeros for predator diversity values at individual point-count stations. In addition, by using sites as the unit of measurement, spatial scales were more consistent with territory sizes of red squirrels (0.3 to 0.8 ha; Price *et al.* 1986, Boutin and Schweiger 1988) and gray jays (40 to 70 ha; Strickland and Ouellet 1993). Analyses were conducted with sites within years pooled because different forest cover types were censused in different years and an array of cover types were needed to obtain maximum variation in bird and predator diversity. Within year analyses were also conducted to determine if trends were consistent within and across years. Regressions for sites using bird and weighted bird diversity were also conducted using square root transformed red squirrel abundance and jay abundance as predictor variables. Use of squirrel and jay abundance separately provided insight into the importance of individual predator species. Because results

differed somewhat between Alberta and Saskatchewan and different predators seemed to be driving these relationships, the above analyses were also conducted within deciduous/mixedwood sites and coniferous sites. Separating forest cover types helped to determine the strength of relationships in habitats typically used versus less used by predators.

The number of negative associations in abundance between pairs of congeneric species with similar foraging ecology was calculated before and after controlling for vegetation and predator abundance. I presumed that competition would be more intense for congeneric species with the same dietary preferences and foraging strategies (Wiens 1989a). Spearman partial correlations were conducted first on species abundance at point-count stations within years. Using forward step-wise multiple regression, residuals for individual species abundance were calculated after controlling vegetation attributes and predator abundance (i.e., squirrels, jays). Vegetation attributes were the same as those used in previous multiple regressions. Partial correlations were conducted again using residuals for species abundance. All analyses were conducted using SAS (1990).

2.3 RESULTS

2.3.1 Literature Review

In total, 142 articles were reviewed (single factor = 103, uncontrolled multiple factors = 25, controlled multiple factors = 14). Avian community responses to habitat features comprised the majority of single factor studies (Table 2.2). Predation studies constituted about 10% of all papers, whereas competition studies ranged from 15-30% with the higher percentage for studies with uncontrolled multiple factors. Articles evaluating effects of food on bird communities tended to examine additional factors and were generally more common than predation but not competition articles. Less than 11% of studies collectively described relationships between bird assemblages and weather and brood parasites. Of 133 articles indicating the number of bird species examined, 17% involved only two species, most of which investigated competition. 18% involved 3-10 species, 58% involved 11 or more species, and 7% involved species

Table 2.2. Summary of published articles that tested for effects of ecological factors on avian abundance and richness.

Ecological factor	Number of articles (percent) ^a	Positive effect (%)	Negative effect (%)	Non-significant effect (%)
Single factor^b				
Habitat structure/composition	67 (55)	99	0	1
Interspecific competitors	16 (15)	0	59	41
Predators	10 (10)	70	20	10
Food	6 (6)	100	0	0
Weather	1 (1)	100	0	0
Brood parasites	3 (3)	100	0	0
Multiple factor - uncontrolled				
Habitat structure/composition	16 (28)	100	0	0
Interspecific competitors	17 (30)	0	65	35
Predators	8 (14)	75	0	25
Food	14 (25)	64	0	36
Weather	2 (4)	100	0	0
Brood parasites	0 (0)	0	0	0
Multiple factor - controlled				
Habitat structure/composition	10 (39)	90	0	10
Interspecific competitors	4 (15)	25	25	50
Predators	3 (12)	100	0	0
Food	6 (23)	100	0	0
Weather	3 (11)	100	0	0
Brood parasites	0 (0)	0	0	0

^a Articles evaluating more than one ecological factor were counted as more than one study.

^b Studies that examined one factor are tabulated separately from those that examined multiple factors that were either uncontrolled or controlled while testing individual factors.

within guilds.

Of 19 articles that examined predation, 68% determined if predators influenced avian community structure and 32% examined behavioral responses to predation risk. Thus, only 9% of 142 articles specifically analyzed effects of predation on community structure, consisting of four artificial nest studies and nine studies using natural communities. Three studies that used artificial nests investigated predator responses to variation in similarity of nest types (Martin 1988b, Hoi and Winkler 1994, Marini 1997). The fourth study formulated predictions about selective forces of red squirrels and gray jays in structuring boreal forest songbird communities based on nest predation rates and predator abundance in deciduous versus coniferous forest (Sieving and Willson 1998). The prediction that coexisting species with similar nest sites will suffer higher predation, tested by most artificial nest experiments, was also supported using natural songbird nests (Martin 1993a, 1996). Moreover, observational data showed that patterns of species coexistence and partitioning of vertical space were more tightly linked to nesting than foraging sites (Martin 1988a,c, 1993a). Two other studies demonstrated that bird abundance and/or composition varied with the presence of raptors (Paine *et al.* 1990, Sodhi 1990, Hakkarainen and Korpimäki 1996), whereas another found that songbird community structure was not related to corvid abundance (Møller 1989). Overall, there was a slight decreasing trend in number of studies addressing predation over time ($r^2 = 0.28$, $P = 0.09$).

2.3.2 Field Study

2.3.2.1 Foothills Natural Region of Alberta

A total of 23,411 individuals of 73 bird species was observed across sites (1990 to 1992): 20 species were unique to Alberta compared to Saskatchewan. The Yellow-rumped Warbler (14.3%), Dark-eyed Junco (9.8%), Swainson's Thrush (8.5%), Chipping Sparrow (6.9%), and Ruby-crowned Kinglet (6.2%) accounted for 46% of all individuals. Red squirrels ($n = 1457$) were two-fold more abundant than gray jays ($n = 717$; Table 2.3). There were almost three-times and four-times as many red squirrels and gray jays, respectively, at sites in Alberta versus Saskatchewan (Table 2.3). Tree

Table 2.3. Mean (\pm SE) bird diversity, predator diversity, and predator abundance in the Foothills Natural Region of Alberta ($n = 98$ sites) and Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan ($n = 60$ sites).

Variable	Alberta	Saskatchewan
Bird diversity ^a	4.1 \pm 0.1	3.6 \pm 0.1
Weighted bird diversity ^b	4.0 \pm 0.1	3.5 \pm 0.1
Diversity of ground-nesters ^c	3.0 \pm 0.1	2.4 \pm 0.1
Predator diversity	1.8 \pm 0.1	1.3 \pm 0.1
Predator abundance (no.)	22.2 \pm 2.1	7.7 \pm 0.8
Red squirrel abundance (no.)	14.9 \pm 1.7	3.6 \pm 0.4
Jay abundance (no.)	7.3 \pm 0.7	4.2 \pm 0.5

^a Shannon-Wiener diversity index was used for all diversity variables.

^b Shannon-Wiener diversity index was weighted by nesting locations.

^c $n = 97$ sites for Alberta.

height and one to three tree species collectively accounted for 27%, 29%, and 49% of variation in bird diversity, weighted bird diversity, and diversity of ground-nesting birds, respectively (Table 2.4). Presence of fir in sites resulted in a greater frequency of occurrence of Boreal Chickadee, Blackburnian Warbler, Brown Creeper, MacGillivray's Warbler, Magnolia Warbler, Pine Grosbeak, Townsend's Warbler, Winter Wren, and White-winged Crossbill.

Controlling for habitat structure and pooling data across years, bird diversity increased curvilinearly with predator diversity (Table 2.5; Fig. 2.1). Similarly, red squirrel and gray jay abundance explained about 37% and 15% of variation in habitat-corrected bird diversity, respectively, but these relationships were linear. Predator diversity and red squirrel abundance also accounted for a significant amount of variation in bird or weighted bird diversity within years. Predator diversity predicted bird diversity in 1991 and 1992 with quadratic and linear models, respectively. Red squirrel abundance was associated with a curvilinear increase in bird diversity in 1990, and a linear increase in weighted bird diversity in 1991.

When forest cover types were analyzed separately, no significant relationships existed within deciduous/mixedwood sites among or within years. For coniferous sites, relationships between all bird response variables and all predator predictor variables were consistently significant across years ($R^2 = 0.09 - 0.52$, $F \geq 5.9$, $P \leq 0.02$), but not within years. Red squirrels were more abundant in coniferous sites (18.0 ± 2.3 SE) than deciduous/mixedwood sites (8.4 ± 1.5). This trend was similar for gray jays with more birds in coniferous (8.6 ± 0.9) than deciduous/mixedwood sites (4.6 ± 0.9).

Initial partial correlations showed a total of five positive species-pair relationships, whereas there were four positive and three negative species-pair relationships across years after controlling variation in vegetation and predator abundance (Table 2.6). Negative associations between congeners were generally difficult to detect except in 1992 when there was a large sample size ($n = 720$). Solitary Vireos had a positive association with Philadelphia and Warbling Vireos in 1990 and 1991, respectively. After controlling for variation due to vegetation and predator abundance, relationships between Solitary Vireos and Philadelphia and Red-eyed Vireos were positive for one

Table 2.4. Regression coefficients and partial correlations for, and percent of variation in bird diversity, explained by vegetation variables based on multiple regression in the Foothills Natural Region of Alberta (1990 to 1992).

Vegetation variable ^a	Regression coefficient	Cumulative r^2	Partial r
Bird diversity			
Tree height (m)	-0.11	0.14	-0.35
Fir species (%)	0.83	0.20	0.29
White spruce (%)	-0.42	0.23	-0.21
Balsam poplar (%)	0.50	0.27	0.02
Weighted bird diversity			
Tree height (m)	-0.13	0.16	-0.37
Fir species (%)	0.88	0.22	0.31
White spruce (%)	-0.42	0.25	-0.20
Balsam poplar (%)	0.53	0.29	0.003
Diversity of ground-nesting birds			
Tree height (m)	-0.48	0.40	-0.68
Trembling aspen (%)	0.77	0.49	0.37

^a Percentage values represent relative frequencies.

Table 2.5. Relationships between residuals of bird diversity versus predator variables in the Foothills Natural Region of Alberta (1990 to 1992).

Predator variable ^a	Overall model			Regression equation ^b
	<i>R</i> ²	<i>F</i>	<i>P</i>	
1990 to 1992 Combined (<i>n</i> = 98)				
Bird diversity				
Predator diversity	0.35	24.99	0.0001	-0.2304 - 0.2418 * diversity + 0.1709 * diversity ²
Resq abundance	0.37	59.29	0.0001	-0.4949 + 0.1405 * resq
Grja abundance	0.15	16.41	0.0001	-0.3794 + 0.143 * grja
Weighted bird diversity				
Predator diversity	0.33	23.82	0.0001	-0.2267 - 0.2487 * diversity + 0.1731 * diversity ²
Resq abundance	0.37	55.24	0.0001	-0.4931 + 0.14 * resq
Grja abundance	0.14	15.98	0.0001	-0.3821 + 0.144 * grja
Diversity of ground-nesting birds^c				
Predator diversity	0.24	14.83	0.0001	-0.1227 - 0.3923 * diversity + 0.2125 * diversity ²
Resq abundance	0.33	22.91	0.0001	-0.1616 - 0.0623 * resq + 0.0239 * resq ²
Grja abundance	0.17	6.20	0.0007	1.4514 - 2.0308 * grja + 0.7628 * grja ² -0.0817 * grja ³
1990 (<i>n</i> = 17)				
Bird diversity				
Predator diversity	0	0.0004	0.98	

Resq abundance	0.63	12.08	0.0009	-0.1162 - 26.509 * resq + 61.481 * resq ²
Grja abundance	0.002	0.03	0.87	
Weighted bird diversity				
Predator diversity	0.001	0.02	0.90	
Resq abundance	0.02	0.25	0.63	
Grja abundance	0.004	0.05	0.82	
Diversity of ground-nesting birds				
Predator diversity	0.02	0.29	0.60	
Resq abundance	0.01	0.20	0.66	
Grja abundance	0.02	0.28	0.61	
Bird diversity				
Predator diversity	0.58	4.15	0.07	-57.535 + 39.607 * diversity - 6.8136 * diversity ²
Resq abundance	0.012	0.08	0.78	
Grja abundance	0.004	0.03	0.87	
Weighted bird diversity				
Predator diversity	0.55	8.66	0.02	-0.0496 + 0.1604 * diversity
Resq abundance	0.54	8.21	0.02	0.1465 - 0.0835 * resq
Grja abundance	0.0003	0.002	0.97	

Diversity of ground-nesting birds

Predator diversity	0.10	0.74	0.42
Resq abundance	0.12	0.99	0.35
Grja abundance	0.04	0.30	0.60

1992 (*n* = 72)**Bird diversity**

Predator diversity	0.04	0.08	0.10	-0.125 + 0.064 * diversity
Resq abundance	0.01	0.92	0.34	
Grja abundance	0.01	0.74	0.39	

Weighted bird diversity

Predator diversity	0.02	1.52	0.22
Resq abundance	0.02	1.21	0.27
Grja abundance	0.0002	0.01	0.91

Diversity of ground-nesting birds

Predator diversity	0.007	0.05	0.83
Resq abundance	0.01	0.78	0.38
Grja abundance	0.02	1.10	0.30

^a Resq = red squirrel, grja = gray jay.^b Regression equations are only shown for those with $P \leq 0.1$. Higher order terms of polynomial models were significant at $P \leq 0.03$.^c For diversity of ground-nesters, $n = 97$ in 1990 to 1992 and $n = 16$ in 1990.

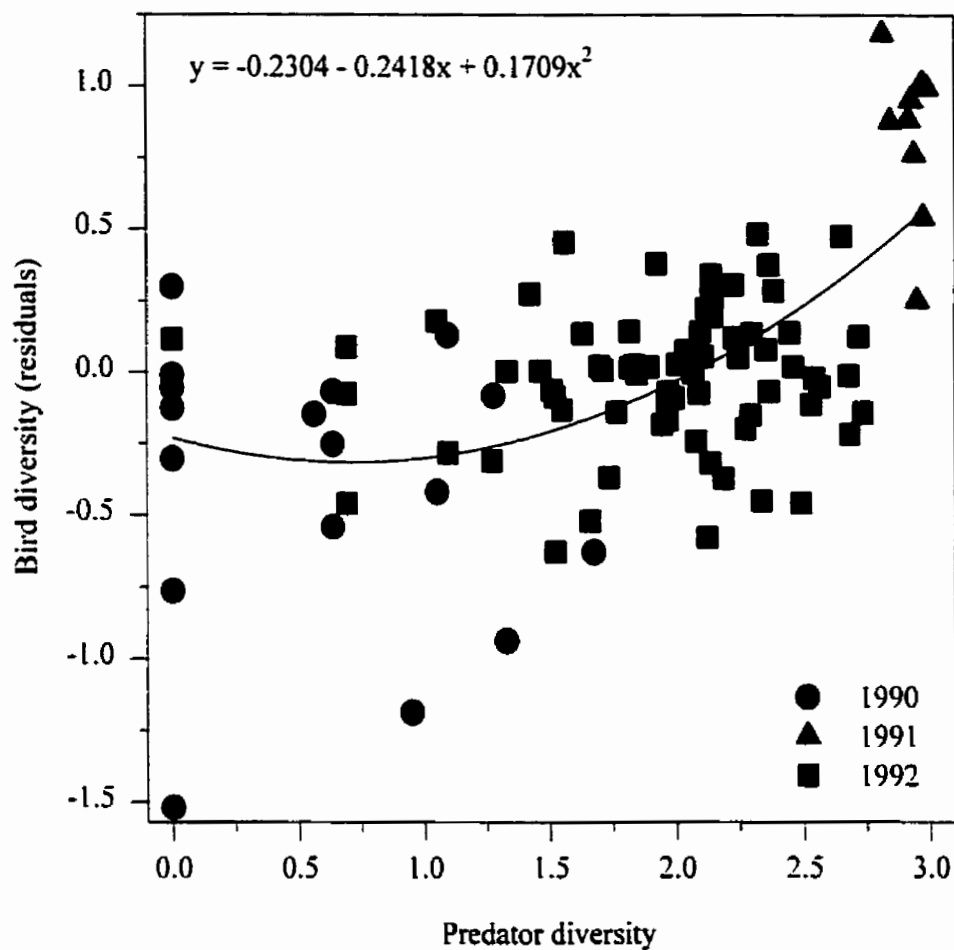


Figure 2.1. Regression of standardized residuals of bird diversity, adjusting for vegetation structure and floristics, relative to predator diversity in the Foothills Natural Region of Alberta (1990 to 1992).

Table 2.6. Partial correlations between pairs of avian congeners belonging to the same foraging guild before and after controlling for vegetation and predator abundance at point-count stations in the Foothills Natural Region of Alberta (1990 to 1992).

	1990	1991	1992	1990	1991	1992	1990	1991	1992
Warblers - <i>Dendroica</i>									
	BLWA^a			TOWA			YEWa		
TOWA ^b			-0.005						
			0.46***						
YEWa			-0.002			-0.006			
			-0.13***			0.15***			
YRWA			0.02			0.05			-0.07
			-0.04			0.03			0.01
Flycatchers - <i>Empidonax</i>									
	ALFL			HAFL			LEFL		
HAFL			0.02						
			0.03						
LEFL		0.02	0.15***			0.12**			
	-0.07	0.13	0.004			0.46			
YBFL	-0.09	0.26**	-0.02			-0.03	-0.08	0.18	0.05
	-0.20	-0.04	0.06			-0.21***	0.08	-0.007	0.31
Vireos - <i>Vireo</i>									
	REVI			PHVI			SOVI		
PHVI									
	-0.07								
	-0.10								
SOVI	0.06		-0.02			0.29*			
	0.03		0.09*			0.39***			
WAVI	0.09		-0.07			0.20	0.09	0.21*	0.05
	0.05		-0.09*			0.06	0.08	0.17	0.02

^a See Appendix B for American Ornithologists' Union codes and scientific names for species.

^b First row contains *r*-values before controlling vegetation and predator abundance. Second row contains *r*-values after controlling vegetation and predator abundance. * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$, **** $P = 0.0001$.

year only and the relationship between Red-eyed and Warbling Vireos became negative in 1992. Positive associations were apparent between three pairs of flycatchers in 1991 or 1992, all of which disappeared when habitat and predators were controlled. However, a negative association existed between Hammond's and Yellow-bellied Flycatchers. When residuals were used, Blackburnian Warblers were positively correlated with Townsend's Warblers but negatively correlated with Yellow Warblers and Townsend's and Yellow Warblers were positively correlated in 1992.

2.3.2.2 *Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan*

There were 6702 detections of 72 bird species during censuses in 1994 and 1995; 17 species were unique to the Saskatchewan data set. The most common species were Yellow-rumped Warbler (8.3%), Tennessee Warbler (8.2%), Pine Siskin (8.0%), White-winged Crossbill (5.6%), Chipping Sparrow (5.2%), Ovenbird (4.8%), and Ruby-crowned Kinglet (4.0%), accounting for 44% of observations. Abundance of jays ($n = 298$) and red squirrels was similar ($n = 273$; Table 2.3). Bird and predator diversities were marginally lower than those in Alberta. Tree height, one shrub species, and four tree species explained 55% and 52% of the variation in bird diversity and weighted bird diversity, respectively (Table 2.7). Two tree species and green alder were the best predictors of the diversity of ground-nesting birds. Bird diversity increased when fir was present, and especially increased Bay-breasted Warblers, Blackburnian Warblers, Black-throated Green Warblers, Brown Creepers, Evening Grosbeaks, and Golden-crowned Kinglets. Greater bird diversity was also associated with green alder through increased frequencies of Bay-breasted Warbler, Cape May Warbler, Evening Grosbeak, Pine Siskin, and Tennessee Warbler.

Controlling for vegetation and pooling data across years, predator diversity accounted for 24%, 22%, and 10% of remaining variation in bird diversity, weighted bird diversity, and diversity of ground-nesting birds respectively (Table 2.8; Fig. 2.2). Trends remained consistent when bird and weighted bird diversity were regressed against abundance of red squirrels and, particularly, jays. When data within years were examined, linear relationships involving predator diversity and jay abundance remained

Table 2.7. Regression coefficients and partial correlations for, and percent of variation in bird diversity, explained by vegetation variables based on multiple regression in Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan (1994 to 1995).

Vegetation variable ^a	Regression coefficient	Cumulative r^2	Partial r
Bird diversity			
Jack pine-canopy (%)	-0.81	0.24	-0.64
White spruce-shrub layer (%)	-0.56	0.30	-0.29
Black spruce-canopy (%)	-1.17	0.37	-0.45
Tree height (m)	-1.19	0.47	-0.41
Green alder (%)	0.26	0.52	0.33
Balsam fir-subcanopy (%)	0.38	0.55	0.24
Weighted bird diversity			
Jack pine-canopy (%)	-0.79	0.22	-0.55
Black spruce-canopy (%)	-0.77	0.28	-0.56
White spruce-shrub layer (%)	-1.30	0.39	-0.34
Rose (%)	-0.34	0.45	-0.28
Tree height (m)	-0.74	0.49	-0.26
Trembling aspen-shrub layer (%)	-0.96	0.52	-0.26
Diversity of ground-nesting birds			
Jack pine-canopy (%)	-1.93	0.27	-0.44
Green alder (%)	1.75	0.37	0.42
Balsam fir-shrub layer (%)	3.40	0.47	0.39

^a Percentage values represent relative frequencies of trees and shrubs.

Table 2.8. Relationships between residuals of bird diversity versus predator variables in Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan (1994 to 1995).

Predator variable ^a	Overall model			Regression equation ^b
	<i>R</i> ²	<i>F</i>	<i>P</i>	
1994 to 1995 Combined (<i>n</i> = 60)				
Bird diversity				
Predator diversity	0.24	18.61	0.0001	-0.3465 + 0.259 * diversity
Resq abundance	0.12	7.69	0.008	-0.3552 + 0.176 * resq
Jay abundance	0.24	17.85	0.0001	-0.5529 + 0.2547 * jay
Weighted bird diversity				
Predator diversity	0.22	16.78	0.0001	-0.335 + 0.2505 * diversity
Resq abundance	0.10	6.29	0.02	-0.3269 + 0.162 * resq
Jay abundance	0.24	18.78	0.0001	-0.5671 + 0.2612 * jay
Diversity of ground-nesting birds				
Predator diversity	0.10	6.56	0.01	-0.2496 + 0.1866 * diversity
Resq abundance	0.03	1.79	0.19	
Jay abundance	0.12	7.69	0.007	-0.4346 + 0.2002 * jay
1994 (<i>n</i> = 40)				
Bird diversity				
Predator diversity	0.11	4.74	0.04	-0.6269 + 0.488 * diversity

Resq abundance	0.02	0.83	0.37	
Jay abundance	0.09	3.95	0.05	-0.3136 + 0.1577 * jay
Weighted bird diversity				
Predator diversity	0.15	6.45	0.02	-0.7874 + 0.5627 * diversity
Resq abundance	0.06	2.24	0.14	
Jay abundance	0.09	3.82	0.06	-0.3388 + 0.1704 * jay
Diversity of ground-nesting birds				
Predator diversity	0.04	1.76	0.19	
Resq abundance	0.01	0.53	0.47	
Jay abundance	0.06	2.47	0.12	
1995 (n = 20)				
Bird diversity				
Predator diversity	0.52	19.25	0.0004	-3.3317 + 1.9422 * diversity
Resq abundance	0.09	1.83	0.19	
Jay abundance	0.61	28.55	0.0001	-0.8942 + 0.3528 * jay
Weighted bird diversity				
Predator diversity	0.71	43.2	0.0001	-4.3038 + 2.5089 * diversity
Resq abundance	0.62	29.91	0.0001	-1.5982 + 0.6027 * resq
Jay abundance	0.37	10.59	0.004	-0.7682 + 0.3031 * jay

Diversity of ground-nesting birds

Predator diversity	0.24	5.76	0.03	-0.5426 + 0.2768 * diversity
Resq abundance	0.15	3.06	0.10	-0.4883 + 0.1841 * resq
Jay abundance	0.18	3.89	0.06	-0.3369 + 0.1329 * jay

^a Resq = red squirrel.

^b Regression equations are only shown for those with a $P \leq 0.1$.

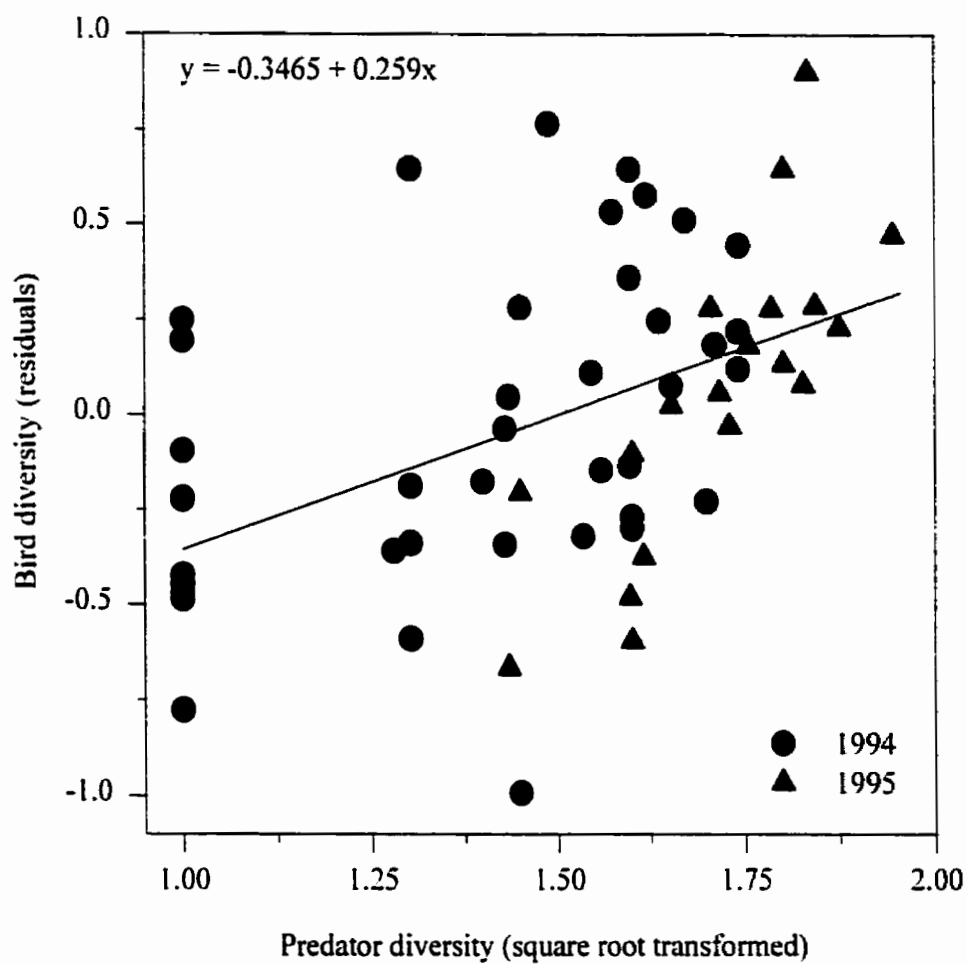


Figure 2.2. Regression of standardized residuals of bird diversity, adjusting for vegetation structure and floristics, relative to predator diversity in Mid-boreal and Churchill River Upland Ecoregions in Saskatchewan (1994 to 1995).

strong, regardless of the response variable. Contrary to Alberta, positive relationships between jay abundance or predator diversity and several bird response variables remained significant across and within years in deciduous/mixedwood sites ($R^2 = 0.22 - 0.60$, $F \geq 4.5$, $P \leq 0.05$). Across years in coniferous sites, jays and red squirrels were both important in producing positive relationships ($R^2 = 0.14 - 0.27$, $F \geq 6.5$, $P \leq 0.02$), though these trends were not upheld within years. Jay abundance was 4.1 ± 1.1 and 4.2 ± 0.5 in deciduous/mixedwood and coniferous sites, respectively. Red squirrels abundance was 5.1 ± 1.1 in deciduous/mixedwood sites and 3.0 ± 0.4 in coniferous sites. All significant regressions were linear, whereas several models from the Alberta data set were quadratic.

There was an initial total of five positive and one negative associations between pairs of congeners in similar foraging guilds in 1994, and four positive and one negative associations in 1995 (Table 2.9). The strongest and most consistent relationship was the positive association between Bay-breasted and Blackburnian Warblers and Black-throated Green and Blackburnian Warblers. After adjusting for effects of vegetation attributes and predator abundance, there was a total of six positive and seven negative associations in 1994, and four positive and two negative associations in 1995. Of 11 initial associations, seven remained significant in the same direction and one changed direction after accounting for habitat and predators. Pairs of species that were negatively associated were confined to warblers: Black-throated Green/Blackburnian, Black-throated Green/Bay-breasted, Black-throated Green/Cape-May, Black-throated Green/Palm, Blackburnian/Cape-May, Blackburnian/Magnolia, Cape-May/Palm. There was no consistency between years for most associations. Relationships of Black-throated Green versus Blackburnian warblers and Black-throated Green versus Palm Warblers were negative in 1994 but positive in 1995.

2.4 DISCUSSION

2.4.1 Literature Review

My literature search (1988 to 1998) summarized research into the hypotheses that have typically been evoked to explain the structure of bird communities. As in the past,

Table 2.9. Partial correlations between pairs of avian congeners belonging to the same foraging guild before and after controlling for vegetation and predator abundance at point count stations in Mid-boreal and Churchill Upland Ecoregions of Saskatchewan (1994 to 1995).

	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
Warblers - <i>Dendroica</i>												
BBWA ^a												
BLWA ^b	0.33 ^{****}	0.31 ^{***}										
	0.19 ^{**}	0.13										
BTGW	0.09	-0.06	0.43 ^{****}	0.17 [*]								
	0.33 ^{****}	-0.24 ^{**}	-0.06 [*]	0.44 ^{****}								
CMWA	-0.08	0.11	0.06	-0.11	0.05	-0.08						
	0.03	0.1	-0.45 ^{****}	-0.06	-0.29 ^{****}	0.05						
CSWA	-0.03	-0.04	-0.08	0.008	0.12	-0.01	-0.02	-0.1				
	0.08	-0.05	-0.09	-0.21 [*]	0.06	0.11	-0.17 [*]	-0.08				
MAWA	-0.004	-0.08	-0.14 [*]	-0.07	0.15 [*]	-0.07	-0.07	-0.1	0.02	0.17		
	0.03	-0.003	-0.16 [*]	-0.12	0.02	-0.08	-0.12	-0.05	0.09	0.28 ^{**}		
PAWA	0.01	0.01	-0.11	-0.08	-0.07	0.31 ^{***}	-0.06	-0.004	-0.06	0.002	-0.04	-0.04
	-0.04	0.05	0.1	-0.13	-0.15 [*]	0.44 ^{****}	-0.16 [*]	-0.08	0.03	0.13	-0.09	0.07
YRWA	-0.07	-0.1	0.07	-0.03	-0.08	0.08	-0.04	0.11	-0.04	0.04	-0.13	-0.04
	0.02	-0.07	0.14 [*]	-0.11	0.07	-0.02	0.07	0.11	0.04	-0.04	-0.06	-0.06
											-0.06	-0.002
Warblers - <i>Vermivora</i>												
NAWA												
OCWA												
	0.19 ^{**}											
	0.47 ^{****}											

TEWA	0.07		0.12	-0.05
	0.12		-0.05	-0.1
Flycatchers - <i>Empidonax</i>				
	ALFL		LEFL	
LEFL	0.08	0.32***		
	0.17*	0.41****		
YBFL	-0.07	-0.02	-0.03	-0.005
	0.03	-0.1	-0.13	0.14
Vireos - <i>Vireo</i>				
	REVI		PHVI	
PHVI	0.04	-0.17*		
	-0.02	-0.1		
SOVI	-0.08	0.1	0.19**	0.05
	-0.13	-0.06	0.17*	0.003

^a See Appendix B for American Ornithologists' Union codes and scientific names for species.

^b First row contains *r*-values before controlling vegetation and predator abundance. Second row contains *r*-values before controlling vegetation and predator abundance. * *P* = 0.05, ** *P* = 0.01, *** *P* = 0.001, **** *P* = 0.0001.

most current studies investigating mechanisms driving avian community patterns have focused on the relationship between avian diversity and proximate factors involving general vegetation structure, substrates, and elevation. Testing predictions arising from interspecific competition theory also continued to be a key research area when evaluating underlying processes, but many experimental tests of the influence of competition targeted either behavior or fitness components of individuals rather than community-level interactions (Goldberg 1994). Despite many references, prior to 1988, to predation as an alternative explanation in the structuring of avian communities, only a limited number of tests of the hypothesis have been conducted since that time, nine (6%) of which used natural nests. Though considerable headway has been made in evaluating the importance of predation in avian community patterns during the last decade, the amount of research was still substantially less than that addressing habitat structure and competition, and new contributions were the work of only a few key investigators. Most predation studies provided evidence consistent with the hypothesis that predators may diversify bird assemblages and controlling additional factors may lead to even stronger patterns consistent with the hypothesis. Effects of competition on bird communities were less clear, particularly when factors other than competition were controlled (Table 2.2). Contrasting results for predation and competition could be an artifact of the number of studies evaluating each ecological process, but evidence for the importance of predation clearly indicated it is a process to be recognized and further testing is required.

There were two major areas of research aimed at understanding predation as a force in avian communities. Most articles on predation presumed effects on avian community structure were mediated directly by predation, primarily at the nest. A number of these studies showed the possibility of predator-mediated coexistence for songbirds. However, most progress in assessing the effects of nest predation on bird community patterns has been forged by one researcher and, consequently, is restricted in geographical range (Martin 1988a,b,c, 1993a, 1996). Future research needs to address the importance of predation in a variety of geographical locations (due to variation in climate, physiognomy, and historical factors), and ultimately, determine whether clear and repeatable patterns exist in different bird communities. Other predation studies

contended that predation on adult birds is ecologically insignificant, based on the premise that community structure is mediated indirectly through changes in predation risk and, subsequently, changes in prey behavior. Of studies that assessed how predation risk affected habitat selection by birds, there was conflicting evidence for the importance of behavioral traits used in anti-predatory escape tactics, such as distance to protective cover and vigilance while foraging (Lima and Valone 1991, Watts 1991, Suhonen *et al.* 1994, Repasky 1996). Overall, the literature review demonstrated that the predation hypothesis has received limited testing and research is needed to investigate predator-mediated coexistence of natural songbird communities.

2.4.2 Vegetation Structure And Floristics

Vegetation structure and floristics accounted for about 30-50% of the variation in bird diversity in Alberta and Saskatchewan, supporting previous studies about the importance of habitat in structuring avian communities (MacArthur and MacArthur 1961, Karr and Roth 1971, Willson 1974, Desrochers *et al.* 1998). In my study, the amount of variation explained by habitat was somewhat lower than found in other studies (James 1971, Rotenberry and Wiens 1980, James and Warner 1982, Anderson *et al.* 1983), possibly because model variables reflected floristics more than structural complexity or foliage volume, or because a more restricted range of habitat types was sampled (Cody 1974, Willson 1974, Mills *et al.* 1991). In Alberta, tree height, the major structural variable, accounted for most variation in bird diversity. Generally, tree height increases with stand-age as does vertical and horizontal heterogeneity (Schieck *et al.* 1995, James and Warner 1982); however, contrary to expectations, bird diversity decreased as tree height increased on both study areas. Sites with low tree heights may have been more heterogeneous in vegetation due to association with gaps in the canopy such as clearings, bogs, residual patches in post-logging sites, and two-pass clearcutting where portions of the same site were cut 10-20 years apart. This suggests spatial horizontal heterogeneity or patchiness may be as important as vertical structure of foliage layers in influencing the organization of avian communities (Rice *et al.* 1984, Derleth *et al.* 1989). Taller trees were also associated with older even-aged coniferous

sites. Consistent with previous findings, bird diversity in my study tended to increase with increasing amounts of deciduous trees and decrease with increasing amounts of coniferous trees (James and Wamer 1982, Willson and Comet 1996a,b, Berg 1997). Trembling aspen often occurred with white spruce in the canopy, subcanopy, and shrub layer, partially explaining its negative association with avian diversity. Rose was closely associated with sites containing jack pine, and alder with sites dominated by white birch, leading to decreased and increased avian diversity, respectively. Alder may have provided a more structurally sound foraging and nesting substrate than rose.

Foliage substrates and density are determining factors in the availability, quality, and distribution of food, foraging niche space, and nesting sites, while floristics are also key for species-specific choices of foraging and nesting substrates (Holmes and Robinson 1981, Martin and Roper 1988, Kelly 1993). However, it is not clear in my study whether increased diversity was a function of complex habitats providing a greater diversity of foraging sites or nesting sites. Other studies have indicated that correlations between bird species and vegetation appear stronger for nesting height and substrates than for foraging (Martin 1988a,b,c; Sedgwick and Knopf 1992, Steele 1993, Matsuoka *et al.* 1997b).

2.4.3 Predation Hypothesis

The range of variation in bird diversity accounted for by vegetation was comparable to other studies (Collins *et al.* 1982, Collins 1983), yet relative amounts of variation explained by vegetation and predators were surprising. Predators accounted for virtually the same amount of variation in bird diversity as did vegetation in Alberta, but only explained about one-half of the variation in bird diversity in Saskatchewan where predator abundance was considerably lower. The gradient of predator diversity was also strongly tied to variation in habitat, with more squirrels and jays in old spruce stands. After controlling for vegetation effects on bird species diversity, bird diversity increased with increased predator diversity, consistent with the hypothesis that predators reduced the similarity of coexisting species. In Alberta, when analyses were confined to conifer stands, where red squirrels typically reside, the pattern was repeatable. Moreover, the

most abundant predators, red squirrels in Alberta and jays in Saskatchewan, accounted for the highest amount of residual variation in bird diversity when predators were analyzed separately. This suggests that coexisting bird species with similar nest niches perceived more predators as a greater risk factor and located elsewhere or that these predators were adept at destroying nests and abundance of individual predator species was a primary factor determining nest losses. However, further work is needed to test these ideas. Testing the predation hypothesis by pooling data across years yielded polynomial regression models for predator diversity in Alberta that accounted for an additional 10% of variation in bird diversity compared to linear models. This supports contentions that many ecological relationships are not simply linear or monotonic (Meents *et al.* 1983, Best and Stauffer 1986).

Because my analyses were based on observational data, my study provides only partial evidence for predators structuring avian communities under natural conditions. In other studies, songbirds with similar nesting habits were dispersed more evenly among vertical vegetation layers than expected based on their foraging behavior, and habitat choice of individual species was more strongly influenced by nesting than foraging sites, lending greater support to the predation versus competition hypothesis (Martin 1988a, Steele 1993, Matsuoka *et al.* 1997). Martin (1993a, 1996) showed that predation on nests of forest songbird species was higher when nesting locations were more similar to those of coexisting species, which may result in more diverse songbird communities. Patterns were also detected when predators responded to species-rich and species-poor assemblages of artificial nests in mixed-conifer and eastern hardwood forests (Martin 1988b, Marini 1997), although not in northern boreal forest (Chapter 3, Rangen *et al.*, submitted manuscript). Conversely, Abbott *et al.* (1977) found that no clear patterns existed between variation in finch abundance or diversity and the number of predator species present on islands in the Galápagos.

Spatial scales used in investigations appear to influence the strength and consistency of evidence for the process of predation, just as they do the interpretation of species assemblage, abundance, and distributional patterns. Predation affected species coexistence in artificial and natural nest studies at a local scale in Arizona (Martin

1988b, 1993a, 1996), but only at a landscape scale in Illinois using artificial nests (Marini 1997). In my study, predation accounted for more of the remaining variation in bird diversity, when examined at a site versus station level, supporting Marini's (1997) findings. Because predation can often be a local phenomenon, detecting interactions between predation and avian community structure at larger spatial scales should generally become more difficult as additional mechanisms interact. Furthermore, difficulties may arise when attempting to understand patterns observed at one spatial scale when underlying mechanisms are operating at another (Levin 1992).

My conclusions that results are consistent with the predation hypothesis rest on the assumption that red squirrels and jays specialize on nest types and locations and that predation is density-dependent in boreal forest. Jays typically destroy more above-ground than ground nests whereas red squirrels depredate similar proportions of each, yet, overall, both predators are opportunistic foragers (Chapter 4, Rangen *et al.* 1999). Generalist foraging strategies of squirrels and jays have likely evolved in response to the extensive variability in boreal forest ecosystems. It has also been argued that, unlike corvids, squirrels do not have territories large enough for individuals to respond to the full range of heterogeneity in nest placement and predation by squirrels may be density-independent (Reitsma 1992, Pelech 1999, Schmidt and Whelan 1999). Thus, selective nest predation by individual predator species may not be sufficiently intense to cause nest-niche diversification and, subsequently, diversification of bird communities over evolutionary time. However, birds may still have a phenotypic response, such as shifts in nest-site characteristics, to episodic selection by predators. In this manner, predators may contribute to contemporary ecological patterns, albeit not via natural selection. This scenario may arise if predation is intense occasionally, yet is relatively unimportant compared to other factors in determining individual fitness or community attributes (Wiens 1989b). Ultimately, environmental variation, food-based competition, and biogeographical and evolutionary histories of avian species probably contributed to observed patterns of avian community assemblage.

2.4.4 Alternative Hypotheses

Because the relationship between predator diversity and songbird diversity was correlative, and because vegetation was the only other factor that was measured directly, alternative hypotheses may also account for the detected pattern. If rich food sources are available, competition theory predicts diversification of bird communities by existing bird species specializing in their foraging niches and, subsequently, leaving some niches vacant for new species or by habitats with previously marginal resources becoming available to new species (MacArthur 1970, 1972). Hence, intense competition reduces bird diversity, the opposite prediction of selective predation. Therefore, if competition was operating synergistically with predation, it should theoretically weaken or mask the observed positive relationship between predator abundance and bird diversity. Apparently, however, this was not the case. Because negative associations between species-pairs were not consistent from year to year, if competition was occurring, it was likely an episodic rather than continuous event with birds responding to variability in local resource levels (Wiens 1977, 1983). Moreover, partialing out vegetation may have removed habitat affinities that directly reflected results of current or past competition (Gotelli *et al.* 1997).

Across years and study areas there were 12 negative associations between congeners in the same foraging guild after habitat and predators were statistically controlled, potentially indicating the process of competition was occurring or had occurred in the past. Lower population densities in west-central Alberta versus central Saskatchewan may account for the increased number of negative associations in Saskatchewan (Hobson and Bayne 1997, Farr 1995, Rangen unpublished data), as competition may be more intense when high densities lead to limited resources. Black-throated Green Warblers were negatively correlated with four congeners. This species has relatively stereotyped foraging patterns compared to Bay-breasted, Blackburnian, Cape-May, and Magnolia warblers (MacArthur 1958, Hall 1994, Williams 1996, Baltz and Latta 1998) and is socially dominant over Blackburnian and Magnolia Warblers (Morse 1971, 1976, Sabo 1980). The abundance and distribution of Cape-May and Bay-breasted Warblers are closely tied to their high responsiveness to outbreaks of

lepidopteran larvae; consequently, they may be competitively inferior to congeners in non-epidemic years (Rabenold 1978, Williams 1996, Baltz and Latta 1998). In outbreak years, these two species can replace those with poor foraging plasticity (Morse 1971). This may partially explain negative associations between Cape-May Warblers and four congeners (i.e., Black-throated Green, Blackburnian, Chestnut-sided, and Palm Warblers) and Bay-breasted Warblers and one congener (i.e., Black-throated Green Warbler) as La Ronge sites in Saskatchewan were situated in a landscape with pockets of elevated spruce budworm levels (Hobson 1996).

Food levels potentially comprised the gradient underlying predator abundance and bird diversity. Positive associations between congeners were more prevalent than negative associations, possibly due to species concentrating in areas where food was abundant or species responded similarly to an unmeasured habitat variable that was correlated with food abundance (Mountainspring and Scott 1985). Some researchers argue that food shortages and competition are uncommon for songbirds in summer but rather these factors are considerably more important on wintering grounds (Martin 1987b).

Relationships in Figures 1 and 2 may also be expected with a decrease in environmental variation due to physiologically intolerant species and species with little behavioral plasticity in feeding habits or nesting locations joining the community (Sabo and Holmes 1983). However, others contend that seasonal migrant birds of temperate forests segregate more strongly by habitat than by elevation or climate (Able and Noon 1976, Telleria *et al.* 1992).

Overall, my evidence for the predation hypothesis was based on observation rather than experiment and, therefore, has limited control over additional sources of variation, other than vegetation. Future studies should use experimental manipulations (removals-additions) to create variation in predator levels. Bird diversity could then be measured as a response variable using point-counts, with the prediction that predator abundance should be positively associated with songbird diversity. Such a relationship may take several years to document to allow for time lags in the response of breeding birds to changes in predator communities but also for behavioral traits of songbirds such as site

fidelity. Also, shifts in nesting substrates or nest placement could be monitored for an array of songbirds with similar and dissimilar nesting sites to determine if nest sites are more similar among coexisting species when predation pressure is low. Artificial nest experiments that evaluate the response of predators to similar and dissimilar nesting assemblages could also help identify whether predators promote nest-site partitioning, even though these studies likely cannot completely resolve the role of predation under natural conditions (Martin 1988b, Marini 1997, see Chapter 3, Rangen *et al.* submitted manuscript).

2.4.5 Conclusions

A positive relationship was found between bird diversity and predator diversity, a pattern of avian species coexistence that was in accordance with that predicted by the predation hypothesis. The preponderance of non-significant and positive versus negative associations between congeneric species with similar foraging strategies further supported my inference that competition was not a strong process. Because my results indicate that predation may be a significant process structuring avian communities, further research should emphasize manipulative experiments that isolate predators and other influential factors, advance our understanding of predator behavior, and focus on shifts in nest-site selection in response to predators (Martin 1998, Pelech 1999).

3. PREDATOR RESPONSES TO SIMILARITY AND DISPERSION OF ARTIFICIAL NEST SITES: IMPLICATIONS FOR THE STRUCTURE OF BOREAL FOREST SONGBIRD COMMUNITIES

3.1 INTRODUCTION

A general goal of avian evolutionary ecology is to understand mechanisms driving patterns of community organization (Wiens 1989a, Martin 1988a). Hypotheses advanced to explain the structure of avian communities have focused primarily on interspecific competition (MacArthur 1965, Schoener 1974, Wiens 1989a) and food limitation (Holmes and Sturges 1975; Martin 1987b, 1991). However, recent research has shown that predation might also be an important factor influencing the evolution of forest songbird community structure (Martin 1988a,b,c; Lima and Valone 1991, Suhonen *et al.* 1994, Forsman *et al.* 1998, Norrdahl and Korpimäki 1998, Sieving and Willson 1998). Although predation is the primary cause of nesting mortality (Ricklefs 1969, Martin 1992), anti-predator strategies employed by birds generally have been neglected as factors structuring avian communities (Martin 1988a, Holmes 1990).

Coexistence of species, or the occurrence of different genetic morphs within a species, may be mediated by predation, as previously documented for grassland plants, intertidal invertebrates, and zooplankton (Caswell 1978). Assuming that predation of songbird nests is density-dependent and predators can specialize on nest types, predators may respond to accumulating densities of similar nesting songbird species as though they were one species (Martin 1988a). Thus, as the number of similar species increases in abundance, each species may, in turn, suffer a greater rate of nest predation. Predation may then provide a selective pressure for coexisting species to select different nest types and locations, presumably within constraints of stereotypic nest placement that arises from a species' evolutionary history (Martin 1993a). Such partitioning of nesting sites may yield a more diverse bird community that, in turn, forces predators to search more

substrates and height levels, inhibiting the development of predator search images, and decreasing predator searching efficiency (Martin 1988b, 1993a).

Predation pressure may favor coexisting songbirds with different nest types and locations, but also species with nests that are well spaced from neighbors. For this to occur, predators must concentrate their search efforts after cueing on nests, resulting in closely spaced nests incurring heavier predation (Tinbergen *et al.* 1967, Sonerud 1985). Some studies using artificial and natural nests, of a variety of avian taxonomic groups, have reported density-dependent predation (Fretwell 1972, Page *et al.* 1983, Esler and Grand 1993, Hogstad 1995, Larivière and Messier 1998), whereas others have found no relationship between predation rates and nest density (Boag *et al.* 1984, Zimmerman 1984, O'Reilly and Hannon 1989, Andrén 1991, Reitsma 1992). Nonetheless, few studies have examined predator responses to nest dispersion patterns of songbirds (Picman 1988, Major *et al.* 1994).

For evolution of songbird nest placement to occur in response to predation on individuals, behavioral, morphological, or physiological traits associated with nest-site selection and subsequent avian community organization must have a genetic basis (Jaenike and Holt 1991). Assessing patterns of songbird species coexistence and nest-spacing provides a first step in understanding nest-site selection and the resulting organization of the avian community. Such patterns are best examined by measuring fitness components (e.g., nest success) because estimates of density and abundance are less likely to be positively correlated with preferred habitat (Van Horne 1983, Pulliam 1988, Vickery *et al.* 1992b). Also, nest predation, rather than predator presence or abundance (Møller 1988), tends to elicit a strong adaptive response with birds shifting nesting locations following failure or changing territories the same or following breeding season (Jackson *et al.* 1989, Morton *et al.* 1993, Haas 1998). A second step is to determine whether patterns are, in fact, being shaped by the process of natural selection, which has been neglected in most nest-site selection studies (Clark and Shutler 1999). This step can be achieved by relating variation in reproductive performance to variation in microhabitat quality and showing adaptation to variation in fitness (Endler 1986, Martin 1998). In all forms of selection, whether stabilizing,

directional, or disruptive, responses by birds to selection pressures may be considered adaptive when more nests, with higher reproductive success, are subsequently placed in specific portions of a habitat gradient.

I examined predator responses to assemblages of artificial songbird nests that were placed along a gradient of variance in vegetation and differed in the number of coexisting songbird species. I also investigated the influence of clumped and random nest distributions on survival of artificial shrub nests. Because it is difficult to directly test hypotheses that nest predators shape forest songbird community patterns through bird species coexistence and nest spacing (hereafter, predation hypothesis), I evaluated whether predators were more successful at detecting nests in sites with similar vegetation or nests that were spatially clumped. I predicted that (1) as variance in nest-site vegetation increased among nest predation plots, predation would decrease, and that (2) following predation, variance in nest-site vegetation (of surviving nests only) would be high among nest predation plots with high predation. Variance in vegetation at nest sites was also expected to be more for surviving versus non-surviving or randomly selected nests. Two-species nest assemblages and clumped nests were predicted to suffer higher predation than three-species assemblages and randomly distributed nests, respectively.

3.2 STUDY AREA AND METHODS

Plots were located in the (Boreal) Lower Foothills Natural Region of Alberta (elevation 1,060 to 1,170 m), approximately 25 km north of Marlboro (53°31'N, 116°45'W), and were of post-logging origin (1970 to 1973). Stands were dominated by trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), fir (*Abies* spp.), and balsam poplar (*P. balsamifera*) comprised most of the remaining canopy. The understory was characterized, in decreasing importance, by willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), low-bush cranberry (*Viburnum edule*), *Ribes* (spp.), and wild rose (*Rosa* spp.).

3.2.1 Response Of Predators To Similarity In Nest-Site Vegetation

Commercial wicker nests (10 cm outside diameter and 6 cm deep) were dipped in

mud, air-dried, and lined with dry grass one week prior to use. Nests were baited with one Japanese Quail (*Coturnix japonica*) and one plasticine egg painted to resemble a quail egg. Quail eggs were washed with tap water prior to use to reduce olfactory cues; this was unnecessary for plasticine eggs as they were made and handled only using rubber gloves.

Six and 10 mixedwood forest stands were selected in 1995 and 1996, respectively, and, in each, I established nest plots (100 m x 100 m), placed at least 800 m apart. Two stands were used in both 1995 and 1996, but nest plots were separated by a minimum of 150 m between years. In 1995 (6 to 18 June), a total of 150 ground nests was deployed with 25 nests per plot. Twenty ground nests were deployed per plot in 1996 (2 to 4 July), totaling 200 nests. At each plot, nests were randomly assigned to grid coordinates (10 m x 10 m) marked by flagging tape, and subsequently deployed in vegetation that characterized nesting microhabitats of seven ground-nesting songbirds in my study area (i.e., Dark-eyed Junco, Hermit Thrush, Lincoln's Sparrow, Mourning Warbler, Orange-crowned Warbler, Tennessee Warbler, White-throated Sparrow). (See Appendix B for scientific names of all bird species). Rims of nest bowls were placed flush with the ground. Nests were marked 2 m on either side by flagging tape of the same color as grid coordinate markers to prevent predators from cueing on nest sites. Rubber gloves and boots were worn during nest deployment and checks (Rudnicki and Hunter 1993). Predation rates on wicker nests were measured by examining loss of eggs from nests every three to five days during 12 (1995) or 15 days (1996) of exposure to predators. A predation event was recorded if any egg was penetrated or missing, or if a plasticine egg was marked. Incisor widths and bill marks in plasticine eggs were used to identify predators (Bayne and Hobson 1997).

Vegetation characteristics at nest sites were recorded at the end of the experiment. Visual estimates were calibrated among four observers before data collection. Point-quarter sampling was used to obtain tree (> 3 m tall) and shrub (> 1 m tall) measurements at nest sites (Krebs 1989). The area around each nest was divided into four equal quadrants, and distances to the nearest tree and nearest green alder or willow were measured in each of the four quadrants. Tree and shrub density calculations

followed Krebs (1989). Plant species and height were identified and measured, respectively, for the nearest tree and shrub in each quadrant (trees ± 0.5 m; shrubs ± 0.1 m). Relative abundance of coniferous versus deciduous trees, individual tree species (e.g., trembling aspen, lodgepole pine), and green alder versus willow were calculated based on the frequency of species in the four quadrants. Deciduous and coniferous trees (≤ 3 m) were counted in a 3-m radius around nests. Percent cover of bare ground and rock, grass/sedge, herbs, lichen, litter, moss, shrubs (≤ 1 m), water, and woody debris were estimated visually in a 2-m radius surrounding nests. Heights of nest substrates were measured. Horizontal and vertical concealment of nests were estimated visually 1 m from nests in four cardinal directions as well as 1 m above nests. Horizontal estimates were obtained 90 cm above ground. These estimates were averaged to obtain a single percentage value of each nest obscured by foliage. Tree and shrub closure was measured using a concave spherical densiometer held 110 cm above ground (Lemmon 1956). Subsequent experiments followed above protocols for nest construction, deployment, monitoring, and concealment unless otherwise stated. Concealment of above ground nests in the following experiments also included an estimate of concealment from 1 m below the nest or from ground level if the distance was < 1 m. The densiometer was held at the same height for ground and above-ground nests.

3.2.2 Predator Response To Two- And Three-Species Assemblages

Each assemblage of artificial nests contained 23 nests but differed by the ratio of nest types, not nest number or dispersion. Nest types were chosen to simulate combinations of three common breeding songbird species in my study area, White-throated Sparrows, Hermit Thrushes, and Chipping Sparrows. Nests of these three species were chosen because they permitted ratios of nests within each nest assemblage to fall within the range of ratios of natural densities of these breeding birds recorded on spot-mapping grids in my study area in 1995. Though ratios of nest types were realistic, densities of artificial nests exceeded those of natural nests. Simulated three-species assemblages consisted of 10 White-throated Sparrow, 9 Hermit Thrush, and 4 Chipping Sparrow nests; two-species assemblages comprised 20 White-throated Sparrow and 3

Hermit Thrush nests.

Wicker and natural nests were used to simulate nest types. Wicker nests (9.5 cm outside diameter x 3.8 cm deep) were lined with dry grass and deer hair to simulate White-throated Sparrow nests. Wicker nests were lined with dry grass and feather moss (*Pleurozium schreberi*, *Ptilium crista-castrensis*) to simulate Hermit Thrush nests. Nest linings used were representative of White-throated Sparrow and Hermit Thrush nests found on my study area. Natural nests (collected 1995 to 1997) were used to simulate Chipping Sparrow nests, to maximize concealment of above-ground nests. Similar to natural Chipping Sparrow nests, all natural nests of bird species used were open cups constructed of grass with an ungulate hair lining (i.e., 4 Chipping Sparrow, 5 Clay-colored Sparrow, 12 Dark-eyed Junco, 2 Lincoln's Sparrow, 1 Tennessee Warbler, 6 White-throated Sparrow, 2 Yellow Warbler).

Nests of each songbird species were deployed in nest substrates identified at natural nests of the respective species on my study area. White-throated Sparrow nests were deployed on the ground under low shrubs including low-bush cranberry, black currant (*R. lacustre*), and Labrador tea (*Ledum groenlandicum*) that averaged 0.44 ± 0.20 SE m tall ($n = 16$ nest predation plots). Hermit Thrush nests were deployed at the base of white spruce and fir seedlings (0.70 ± 0.10 m tall, $n = 16$ plots). Chipping Sparrow nests were deployed above-ground (0.63 ± 0.70 m, $n = 8$ plots) in conifers averaging 2.27 ± 0.20 m tall ($n = 8$ plots). Within paired plots (described below), for both experimental assemblages, the same shrub species were used as nest substrates. Shrub species, however, changed from stand to stand due to local changes in vegetation.

Eight mixedwood forest stands were selected in which to establish paired plots (2 ha) in turn separated by 100 m. Plots in separate stands were at least 800 m apart. Nest distributions were allocated randomly to one of the paired plots. Twenty-three nests were deployed per plot, totaling 184 nests per treatment. Nests were deployed (7 to 14 June 1997) at random coordinates in each plot, using numbered cells in a 25 m x 25 m grid. Predation rates on nests were measured by examining loss of eggs from nests every five days during 15 days of exposure to predators. Nest concealment and species and height of nest substrates were recorded. Distance (m) to nearest-neighbor ground

nests or nest trees (for above-ground nests) was recorded.

3.2.3 Predator Response To Clumped Versus Random Distributions Of Shrub Nests

Five mixedwood forest stands were selected in which to establish paired plots (1 ha). One plot of each pair was assigned randomly to a random or clumped nest distribution. Twenty nests were deployed per plot (17 to 20 July 1996). Randomly distributed nests were deployed at random coordinates, using numbered cells in a 10 m x 10 m grid. Four groups of five clumped nests each were deployed in each plot with one group at each corner grid cell. One nest was placed at each corner and one in the center of these grid cells. Nests were placed in a shrub closest to the allocated grid location, which was usually within 2 m. Nests for both distributions were randomly, but equally, allocated to a 0.5 m height class (range 0.5 to 2 m). Predation rates on shrub nests were measured by examining loss of eggs from nests every five days during 10 days of exposure to predators. Nest concealment and distance (m) to nearest-neighbor nests were measured (using the base of nest substrates because some nests were above-ground).

3.2.4 Statistical Analyses

3.2.4.1 *Response Of Predators To Similarity In Nest-Site Vegetation*

To examine the response of predators to similarity in nest-site vegetation, I first used reciprocal averaging (RA) ordination to collapse original measurements of vegetation structure and composition at 344 nests into single axes (Pielou 1984). Reciprocal averaging versus a principal components analysis (PCA) was used because some variables displayed non-linear relationships against derived axes for PCA. Prior to the analysis, variables with zeros in > 50% of the data set were deleted to prevent uncommon variables from disproportionately influencing the analysis (i.e., bare ground and rock, water). Remaining variables (i.e., coniferous trees > 3 m tall, coniferous trees \leq 3 m tall, deciduous trees > 3 m tall, deciduous trees \leq 3 m tall, grass/sedge, green alder, herbs, lichen, litter, lodgepole pine, moss, shrub density, shrub height, tree and shrub closure, tree density, tree height, trembling aspen, willow, woody debris) were

log, arcsine, or square root transformed to improve normality. The interpretation of RA axes was based on the relative sizes of correlations between axes and originally measured variables. Variances and coefficients of variation (CV) in nest-site vegetation for each nest predation plot were calculated using RA1 and RA2 for the 20 to 25 nests per plot. RA1 and RA2 were chosen to represent variance in vegetation among plots in regressions (see below) as they accounted for the majority of variation in nest-site vegetation within plots. However, because these axes characterized tree and shrub species composition rather than microhabitat features surrounding nests, that are presumably important in predator search images, RA analyses were also conducted using only ground vegetation variables.

To evaluate my prediction that predation was directly related to similarity in nest-site vegetation before selection occurred, linear regressions of variance in RA1 and RA2 vegetation scores for all nest sites versus daily nest mortality rate (50%-Mayfield; Mayfield 1975) were conducted using 16 nest predation plots visited 1995 to 1996. To test the prediction that there was a negative relationship between predation and similarity in nest-site vegetation following selection, linear regressions of variance in RA1 and RA2 vegetation scores of successful nest sites versus daily nest mortality rate (50%-Mayfield; Mayfield 1975) were conducted using 15 nest predation plots. One plot was deleted because all nests failed. Examination of residuals and tests of curvilinearity supported the use of linear models. Predictions were best tested with a wide range of nest mortality and variance in nest-site vegetation; therefore, nest predation plots were pooled across years to help achieve this. In addition, analyses were conducted within years and similar results were found, justifying pooling of data.

Interpretations based on two forest stands in both 1995 and 1996 should have been conservative because plots between years were spatially separated within the same stand and new random nest locations were allocated each year. Moreover, nests between years were likely deployed in territories of different individual red squirrels (*Tamiasciurus hudsonicus*) and mice, due to spatial independence but also high turnover of these species (Banfield 1974, Rusch and Reeder 1978). However, to ensure pseudoreplication did not influence analyses, linear regressions were conducted with and

without 1996 plots located in forest stands also containing 1995 plots. R^2 - and P -values were similar for both regressions, thus my results are from analyses including all 16 nest predation plots. Regressions were also conducted using CV in lieu of variance, but again identical results were obtained so only those for variance were reported. Due to inconsistencies in patterns obtained for predator responses to two- and three-species assemblages when nests visited by mice were treated as non-surviving or surviving (see below), the above regressions were also conducted with nests depredated by mice excluded from the analysis. Similarly, results were given for all nest predation plots and variance in RA scores only.

To evaluate whether predators were a selective pressure and, if so, how the process of predation was operating, standardized selection differentials were calculated (Endler 1986). Measures of directional selection and stabilizing/disruptive selection were used to compare distributions of nests along the vegetation gradient that 1) survived versus nests randomly selected from all available nests before predation; and, 2) survived versus those that were destroyed. Standardized selection differentials were derived from means and variances of RA1 and RA2 scores for each group of nests (i.e., non-survivors, survivors, nests selected at random before predation). Tests to detect selection are more sensitive when nests remaining after selection are compared to those that are depredated because the two samples are independent, and means and variances will be less similar than if surviving nests and nests before predation are compared. Therefore, to control for differences in variance between surviving nests and nests before selection by predators due to sample size, random samples of nests before predation, equal in number to surviving nests ($n = 198$), were selected. Fifty iterations of random nest selections with replacement were conducted, and the mean of the mean and mean of the variance were calculated.

3.2.4.2 Predator Response To Two- And Three-Species Assemblages

To examine predator responses to two- and three-species assemblages, nest fate and number of days nests survived (Johnson 1979) were used as response variables in a two-way analysis of covariance (ANCOVA), with species assemblage (i.e., two, three), and

nest type (i.e., White-throated Sparrow, Hermit Thrush, Chipping Sparrow) as main effects, and concealment and nearest-neighbor distance as covariates. Nest predation plots were used as sampling units; thus, plot means for each nest type within each species assemblage ($n = 40$) were used in ANCOVAs. Results for nest fate and number of surviving days were similar; therefore, surviving days were reported only. Home ranges of mice may be only one-fifth to one-tenth the size of my plots (Williams 1955, McCann 1976), precluding mouse exposure to a sufficient number of artificial nests, and subsequent development or use of search images. Hence, mice may not have had the opportunity to specialize in their choice of nests, an assumption necessary for predation pressure to result in partitioning of nest sites (Tinbergen 1960, Sonerud and Fjeld 1987, Ricklefs 1989, Hoi and Winkler 1994). Furthermore, some bird species may be able to defend their nests against mice (Verbeek 1970). Therefore, two additional ANCOVAs were conducted, using nest fate and the number of days nests survived as response variables, where nests depredated by mice were excluded. Trends in rates of predation using number of days surviving were similar to those where all predators were examined; therefore, only predator responses to species assemblages using fate are presented. A Kolmogorov-Smirnov test was used to compare daily nest survival probabilities (Mayfield 1975), accounting for all predator species and all predators excluding mice. Fisher's exact test was used to determine the response of different predator groups to both species assemblages.

3.2.4.3 *Predator Response To Clumped Versus Random Distributions Of Shrub Nests*

To examine predator responses to clumped nest distributions, nest fate and number of days nests survived were used as response variables in a one-way ANCOVA, with nest distribution as a main effect and concealment as a covariate. Nest predation plots were used as sampling units. A Kolmogorov-Smirnov test was used to compare daily survival probabilities. Because clumped nests were equally spaced, effects of nearest-neighbor distances on plot means of fate and number of days nests survived were examined only for random nests using simple linear regression. Because results for nest fate and number of surviving days were the same, only those for surviving days were

reported. Responses of specific predator groups to nest distributions were examined using Fisher's exact test. Statistical tests followed Zar (1984) and were executed on SAS (1990) with a significance level of 0.05.

3.3 RESULTS

3.3.1 Response Of Predators To Similarity In Nest-Site Vegetation

Axis 1 (RA1) accounted for 44% of total variance in ground cover, shrubs, and trees using all nests in 16 nest predation plots and represented a gradient in tree species composition ranging from deciduous (primarily trembling aspen) to coniferous (primarily lodgepole pine) trees (Table 3.1). Axis 2 (RA2) accounted for an additional 20% in total variance, expressing a shift in shrub species composition from willow to green alder. Additional axes were not retained as they each accounted for $\leq 7\%$ of total variation. Plots with high variance in RA1 scores contained individual nest sites represented by pine, mixedwood, or trembling aspen. Some plots with low variance contained individual nest sites that were dominated either by pine or mixedwood, whereas other plots had individual nest sites that were dominated by either aspen or mixedwood. Plots with high variance in RA2 scores had nest sites with green alder, willow, or a mixture of these two species. Low variance plots had nest sites dominated by willow or green alder, both of which were accompanied by a few patches of both shrub species. Using ground cover only, axis 1 (RA1G) comprised 27% of total variance and expressed a gradient in ground vegetation from lichen to grass. Plots with high variance in RA1G scores contained individual nest sites with lichen, grass, or both. Some plots with low variance contained individual nest sites with lichen or lichen and grass, whereas nests in other plots were dominated by grass or grass and lichen.

Before predation occurred, there was no relationship between nest-site similarity across plots, based on RA1, RA2, and RA1G scores, and nest mortality, respectively (RA1: all predators, $r^2 = 0.05$, $P = 0.41$, $n = 16$; nests depredated by mice were excluded, $r^2 = 0.004$, $P = 0.81$, $n = 16$; RA2: all predators, $r^2 = 0.02$, $P = 0.59$, $n = 16$; nests depredated by mice were excluded, $r^2 = 0.01$, $P = 0.70$, $n = 16$; RA1G: all predators, $r^2 = 0.07$, $P = 0.32$, $n = 16$; nests depredated by mice were excluded, $r^2 =$

Table 3.1. Correlations between vegetation variables at all artificial ground nests ($n = 344$) in 16 nest predation plots in boreal mixedwood forest stands in west-central Alberta (1995 to 1996) and reciprocal averaging (RA) axes.

Vegetation variable (%) ^a	RA1 ^{bc}	RA2	RA1G
Coniferous trees > 3 m	0.76	0.25	
Coniferous trees ≤ 3 m (no.)	0.21	-0.07	
Deciduous trees > 3 m	-0.53	-0.19	
Deciduous trees ≤ 3 m (no.)	-0.11	-0.04	
Grass/sedge	-0.01	-0.08	-0.27
Green alder	-0.58	0.85	
Herbs	-0.03	-0.04	-0.06
Lichen	0.24	0.11	0.63
Litter	-0.08	0.08	0.20
Lodgepole pine	0.75	0.25	
Moss	0.25	-0.02	0.45
Shrubs ≤ 1 m	-0.02	0.08	-0.07
Shrub density (/ha)	0.02	0.00	
Shrub height (m)	-0.03	0.02	
Tree and shrub closure	-0.89	0.03	
Tree density (/ha)	-0.04	0.00	
Tree height (m)	-0.01	0.01	
Trembling aspen	-0.66	-0.21	
Willow	0.36	-0.47	
Woody debris	0.00	-0.02	-0.01

^a Variables are represented by relative frequencies (%), unless otherwise shown.

^b Correlations > |0.40| are in bold.

^c RA1 and RA2 were derived using ground cover, shrubs, and trees. RA1G was derived using ground cover only.

0.03, $P = 0.53$, $n = 16$; Fig. 3.1) nor was there after predation occurred, whether nests depredated by mice were excluded or not (RA1: all predators, $r^2 = 0.04$, $P = 0.47$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.005$, $P = 0.81$, $n = 15$; RA2: all predators, $r^2 = 0.02$, $P = 0.65$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.003$, $P = 0.85$, $n = 15$; RA1G: all predators, $r^2 = 0.12$, $P = 0.20$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.002$, $P = 0.89$, $n = 15$; Fig. 3.2). Moreover, based on selection differentials, predation did not lead to increased variance in vegetation at surviving nests compared to non-surviving or randomly selected nests (Table 3.2).

3.3.2 Predator Response To Two- And Three-Species Assemblages

Of the total nests ($n = 368$), 30% ($n = 107$) were considered depredated based on evidence from quail and plasticine eggs. Of these, 64% ($n = 68$) could be attributed to specific predators (mice, 42%; small mammals, 6%; squirrels, 10%; birds, 1%; large mammals, 5%). Small mammals probably include mice and juvenile squirrels that could not be separated based on incisor widths. Large mammals include species larger than red squirrels such as snowshoe hares (*Lepus americanus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and cervids. Using surviving days, all predators combined did not discriminate between species assemblages ($F = 1.6$, $df = 1$ and 34, $P = 0.21$; Table 3.3) and responded similarly to the three nest types ($F = 0.5$, $df = 2$ and 34, $P = 0.59$). Nearest-neighbor effects were not evident ($F = 0.3$, $df = 1$ and 34, $P = 0.59$) nor did concealment differ between successful and failed nests ($F = 3.5$, $df = 1$ and 34, $P = 0.07$). When nests depredated by mice were excluded from analyses and fate was used as a dependent variable, the remaining predators appeared to be more adept at destroying nests of the two-species assemblage ($F = 4.5$, $df = 1$ and 34, $P = 0.04$; Table 3.3) but nest losses of the three songbird species did not differ ($F = 2.0$, $df = 2$ and 34, $P = 0.15$). Nests that were closer together were not more susceptible to predators ($F = 2.1$, $df = 1$ and 34, $P = 0.16$), though poorly concealed nests were ($F = 5.2$, $df = 1$ and 34, $P = 0.03$). Daily survival probabilities over 15 days were similar for two- and three-species assemblages when all predators were combined ($D = 0.3$, $P > 0.5$) or when nests

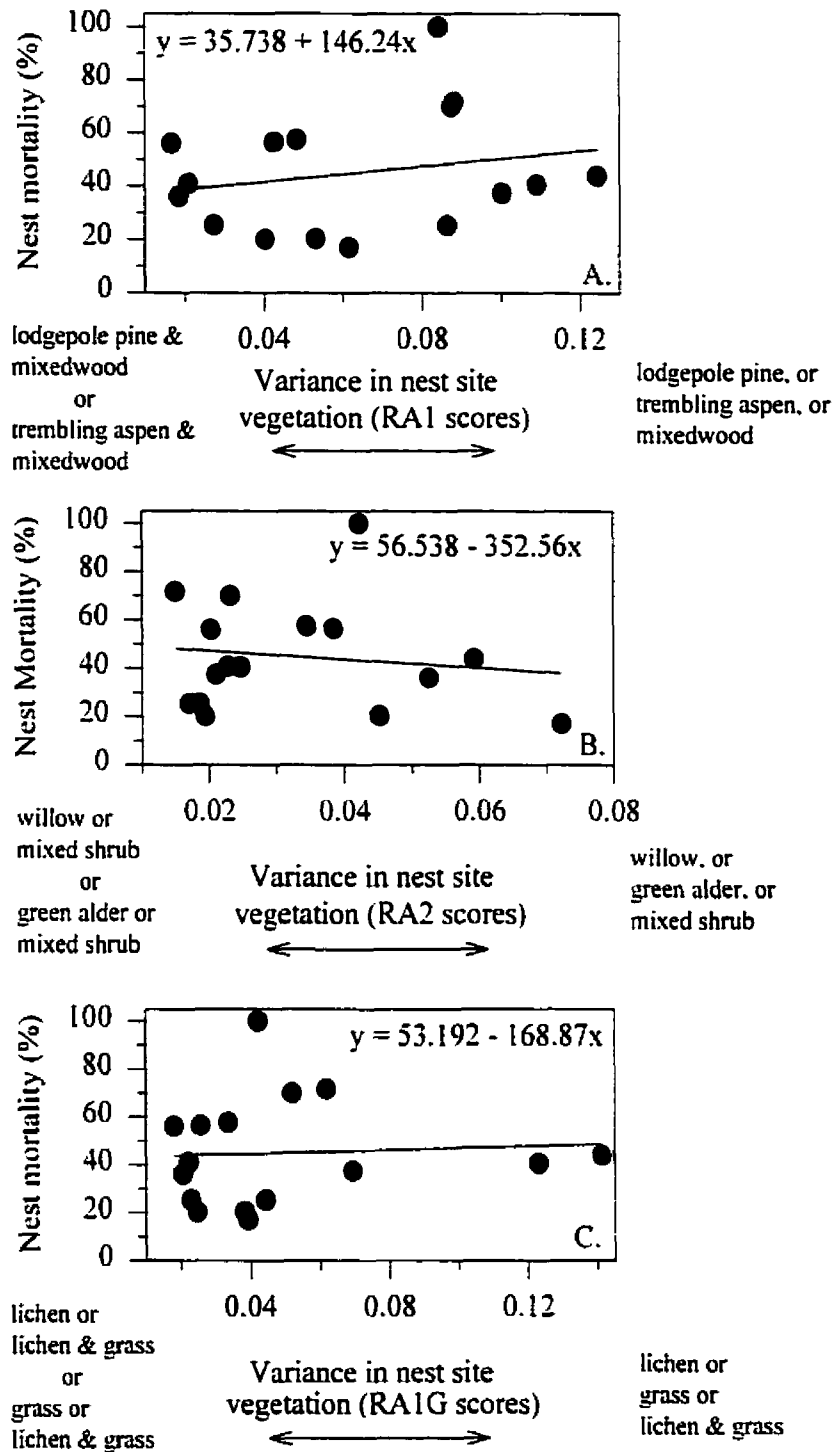


Figure 3.1. Relationship between mortality of all nests and variance in nest-site vegetation across 16 nest predation plots in boreal mixedwood forest stands in west-central Alberta (1995 to 1996). RA1 (A.) and RA2 (B.) scores were derived using ground cover, shrubs, and trees. RA1G (C.) scores were derived only using ground cover. Gradients in variance show vegetation features that dominate individual nest sites within plots.

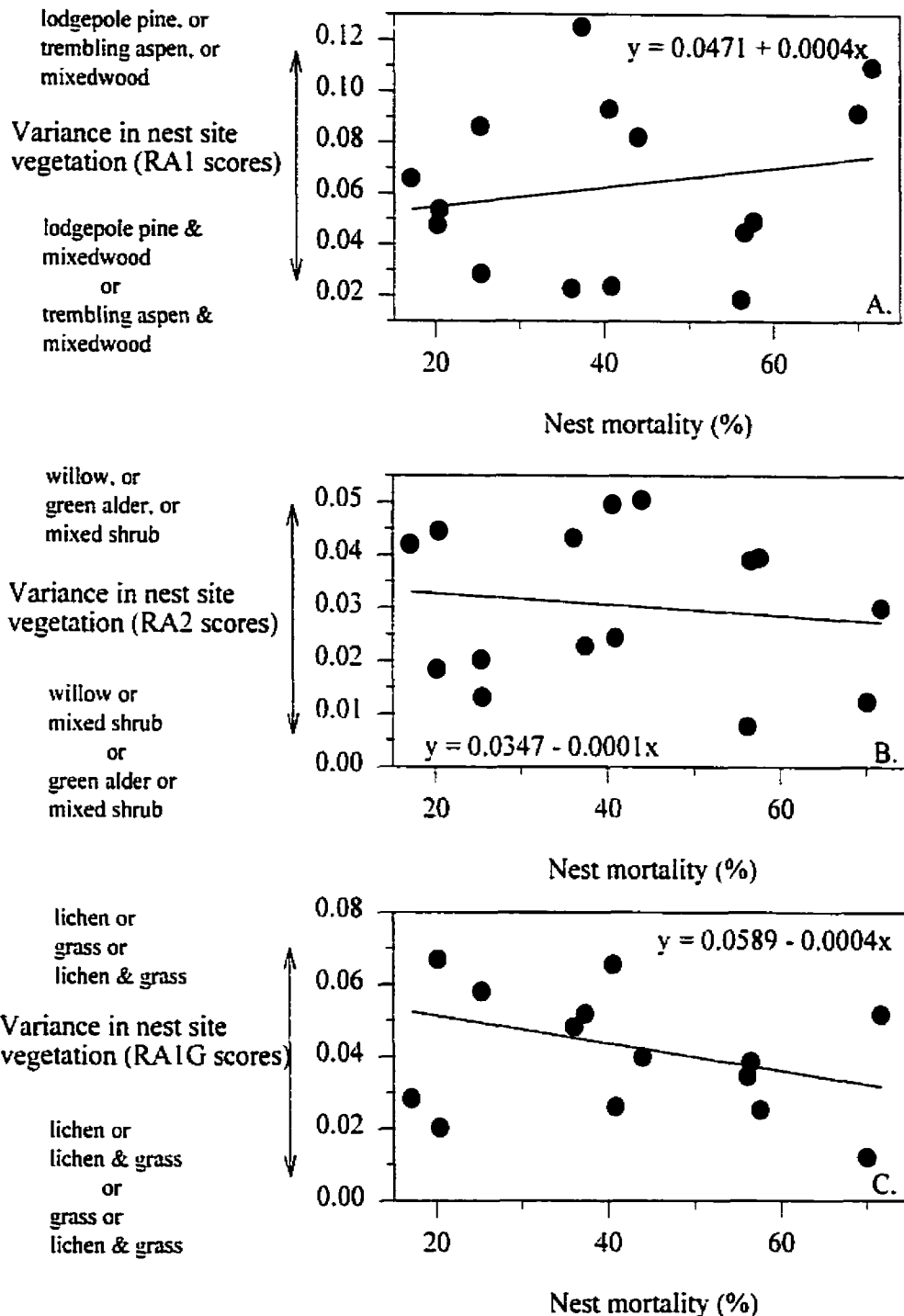


Figure 3.2. Relationship between variance in nest-site vegetation and mortality at surviving nests across 15 nest predation plots in boreal mixedwood forest stands in west-central Alberta (1995 to 1996). RA1 (A.) and RA2 (B.) scores were derived using ground cover, shrubs, and trees. RA1G (C.) scores were derived only using ground cover. Gradients in variance show vegetation features that dominate individual nest sites within plots.

Table 3.2. Standardized directional (i) and stabilizing/disruptive selection differentials (j) for the effect of predation on vegetation similarity at nest sites of artificial ground nests in boreal mixedwood forest stands in west-central Alberta (1995 to 1996). Vegetation similarity was derived from reciprocal averaging ordination axes (RA1 and RA2).

Vegetation similarity	Selection differential			
	i	P	j	P
Survivor versus non-survivor nests				
RA1	-0.85	0.40	1.03	0.42
RA2	0.51	0.84	1.07	0.32
Survivor versus randomly selected nests				
RA1	0.10	0.68	1.02	0.48
RA2	0.19	0.68	1.02	0.48

Table 3.3. Number of days nests survived (mean \pm SE) or fate (mean \pm SE) in parentheses for species assemblage and nest type, nearest-neighbor distances and concealment for successful and failed nests, combining all predators and excluding nests depredated by mice, in boreal mixedwood forest stands in west-central Alberta (June 1997).

Species assemblage ^a		Nest type ^a			Nearest-neighbor distance (m) ^b		Concealment (%) ^b	
Two	Three	White-throated Sparrow	Hermit Thrush	Chipping Sparrow	Successful	Failed	Successful	Failed
All predators								
12.3 \pm 0.6 (1.5 \pm 0.1)	13.3 \pm 0.4 (1.6 \pm 0.1)	12.2 \pm 0.7 (1.5 \pm 0.1)	13.4 \pm 0.7 (1.6 \pm 0.1)	12.8 \pm 0.9 (1.5 \pm 0.1)	26.7 \pm 0.8	25.0 \pm 0.7	87.0 \pm 1.3	81.2 \pm 2.5
Predators excluding mice								
12.8 \pm 0.6 (1.5 \pm 0.1)	13.7 \pm 0.4 (1.7 \pm 0.1)	13.0 \pm 0.7 (1.7 \pm 0.1)	13.8 \pm 0.6 (1.7 \pm 0.1)	12.9 \pm 0.8 (1.5 \pm 0.1)	26.7 \pm 0.7	25.2 \pm 0.8	87.0 \pm 1.3	80.2 \pm 2.5

^a Least square means are reported.

^b Unadjusted means are reported.

depredated by mice were excluded ($D = 0.3$, $P > 0.5$). Squirrels, birds, and mice did not destroy one species assemblage any more than another, nor did one predator group destroy more nests of one species assemblage compared to another predator group (Table 3.4).

3.3.3 Predator Response To Clumped Versus Random Distributions Of Shrub Nests

Forty-nine percent of nests were depredated (98 of 200). About one-half of depredated nests could not be ascribed to a specific predator ($n = 48$). Of the remaining nests, birds destroyed most (34%) followed by small mammals (30%), squirrels (26%), mice (8%), and large mammals (2%). Predators did not depredate more clumped versus random nests by the end of the experiment (random nests, surviving days = 7.2 ± 0.7 SE; clumped nests, surviving days = 7.4 ± 0.7 ; $F = 0.03$, $df = 1$ and 7 , $P = 0.86$) nor during the first 10 days of exposure ($D = 0.17$, $P > 0.5$). Concealment of nests was similar for successful ($54.6 \pm 2.3\%$, $n = 9$) and failed nests ($44.8 \pm 2.5\%$; $F = 3.15$, $df = 1$ and 7 , $P = 0.12$, $n = 10$). Loss of random nests to predators was not related to the proximity of nearest-neighbor nests ($r^2 = 0.20$, $P = 0.44$, $n = 5$; Table 3.5). Avian and mammalian predators did not prey on a greater number of nests of any one nest distribution nor were there differences between birds and mammals with respect to depredation of random and clumped nests (Table 3.6).

3.4 DISCUSSION

3.4.1 Predator Response To Nest-Site Similarity

Whether or not similar communities of simulated nesting songbirds were more susceptible to predation appeared to be closely linked with the composition and abundance of the predator community. Evidence consistent with this hypothesis was strongest with respect to how squirrels and birds depredated two-species assemblages. When mice were included in the analysis, the entire predator community did not differentially destroy two- and three-species assemblages. My result that predators other than mice might favor partitioning of nesting microhabitat supported the idea that search

Table 3.4. Number (percentage) of nests of two- and three-species assemblages ($n = 8$) that were visited by predators in boreal mixedwood forest stands in west-central Alberta (June 1997). A total of 368 nests was deployed.

Species assemblage ^a	Mice	Squirrels	Birds
Two	26 (79)	5 (15)	2 (6)
Three	18 (62)	5 (17)	6 (21)

^a Fisher's exact test; $P = 0.23$.

Table 3.5. Distance (m) (mean \pm SE) to nearest-neighbor nests that survived or failed within random and clumped nest distributions ($n = 5$) in boreal mixedwood forest stands in west-central Alberta (July 1997).

Nest distribution	Surviving	Failed
Random	15.5 \pm 1.23	12.8 \pm 0.77
Clumped	7.1 \pm 0	10.0 \pm 2.91

Table 3.6. Number (percentage) of nests in random and clumped distributions ($n = 5$) visited by predators in boreal mixedwood forest stands in west-central Alberta (July 1997).

Nest distribution	Mice	Squirrels	Small mammals	Birds
Random	2 (8)	8 (31)	7 (27)	9 (34)
Clumped	2 (8)	5 (22)	8 (35)	8 (35)

images based on nest appearance or nest height were probably less important to mice that rely primarily on olfaction for food detection and forage on the ground (Howard *et al.* 1968, Anderson 1986). Similar to my arguments regarding mice, Schmidt and Whelan (1999) contended that territories of squirrels are too small for individuals to detect and respond to the full range of heterogeneity in nest abundance and placement, but those of corvids are large enough to respond to patterns of nest heterogeneity. However, I had insufficient data to test squirrels and corvids separately. Mice are more adept at locating ground nests, squirrels tend to destroy similar numbers of ground and above-ground nests, and birds depredate relatively high numbers of above-ground nests (Chapter 4, Rangen *et al.* 1999). Assuming this, and that predator communities were similar between experimental assemblages, additional predation pressure from avian predators on the three-species assemblage may have counteracted any predisposition of more similar nest sites of the two-species assemblage to be depredated, leading to similar predation rates of the two nest assemblages. Support for this explanation was inconsistent, however, with squirrels and gray jays (*Perisoreus canadensis*) destroying more nests of the two-species assemblage when fate was used as the response variable but not when number of surviving days were used. In contrast, studies suggesting that predators can diversify songbird communities either had both ground and above-ground nests destroyed by the same predator species or nest predators were not identified (Martin 1987b, Marini 1997). Alternatively, if predators of forest songbird nests have evolved as generalists to survive in a highly variable and seasonal environment, it may also be difficult to detect patterns of songbird species coexistence induced by predation, particularly if nest losses are opportunistic (Blancher and Robertson 1985, Andr  n 1995). This may be especially true of boreal forest communities that can encompass considerable range in spatial and temporal variability in stand structure.

Differences between my experimental design and that of comparable studies may have led to contrasting results (Martin 1988b, Marini 1997), but again such distinctions in design can be linked to variation in the predator community. Consequently, differences in predator communities among studies could be a contributing factor to inconsistencies in observed patterns or common predators among studies may have

responded differentially under varying experimental conditions. In earlier studies, trends showing that predators were able to destroy more songbird nests if they had similar nest placements were consistent whether artificial or natural nests were used (Martin 1988b, Marini 1997), a pattern that was only apparent in my study when nests visited by mice were excluded from analyses. Lower predation on the three-species nest assemblage, under these circumstances, may be related to natural nests used for Chipping Sparrows being less conspicuous to squirrels and jays than wicker nests used in the two-species assemblage (but see Martin 1987a). However, because a similar proportion of Chipping Sparrow versus White-throated Sparrow and Hermit Thrush nests was destroyed, this explanation appears weak. Besides nest type, my study was unique in the use of plasticine and quail eggs, as similar experimental designs used quail eggs only (Martin 1988b, Marini 1997). Because mice can be attracted to plasticine eggs (Chapter 5, Rangen *et al.* 2000a; but see Bayne and Hobson 1999) and mice tend to visit more ground than above-ground nests (Graves *et al.* 1988; Chapter 4, Rangen *et al.* 1999), the higher proportion of ground nests in the two-species assemblage may have elevated nest losses, masking an assemblage effect. Moreover, previous experimenters excluded potential effects by mice as members of the predator community by only using quail eggs that are too large to be broken by mice (Roper 1992, Haskell 1995a, DeGraaf and Maier 1996; Chapter 5, Rangen *et al.* 2000a; but see Blight *et al.* 1999). Lastly, variation in nest types and nesting guilds may not have been high enough for predators to discriminate between experimental nest assemblages; thus, a greater range in diversity of nest types or nest guilds might have generated predator responses consistent with Martin's (1988b) hypothesis, as did other investigations that compared different species assemblages (Martin 1988b, Marini 1997).

I have emphasized the importance of understanding the structure of predator communities and behavior of predator species, yet choice of boreal habitats in which to test the predation hypothesis may also be critical. Boreal forest encompasses an array of structural and floristic complexity at both the stand and landscape level (Schieck *et al.* 1995, Hobson and Schieck 1999), while my experiments were restricted to relatively homogeneous mixedwood stands, preventing generalizations across cover types and

seral stages. In structurally simple habitats, predation may initially act to decrease similarity within nesting guilds, but as predation intensifies and the limited number of nest niches in which species can expand are exhausted, coexisting species may be forced to nest in similar locations, increasing similarity of nesting guilds (Menge and Sutherland 1976, Sih *et al.* 1985). Thus, if predators had already forced songbird species to deplete finite nesting options in these stands over evolutionary time, predators may have responded to my experiment as though nest assemblages were very similar. Both predator community composition and boreal forest heterogeneity are related to spatial scale, which can also lead to contradictory results regarding the influence of predators on species coexistence (Marini 1997). Furthermore, if songbirds have not partitioned nesting sites to potentially escape predation, other anti-predator strategies such as behavior, nest spacing, morphology, and life-history traits may be more important in reducing predation risk (Lima and Dill 1990, Major *et al.* 1994, Martin 1995, Lima 1993, Götmark and Post 1996, Swaddle and Lockwood 1998).

3.4.2 Predator Response To Clumped Versus Random Distributions Of Shrub Nests

Predator responses to variation in nest spacing patterns may also be obscured by the composition of the predator community (Picman 1988, Major *et al.* 1994, Hogstad 1995). Selection pressures placed on nesting songbirds vary with type of predator, particularly avian predators and ground-dwelling mammals, thereby preventing stereotyped anti-predator strategies (i.e., non-clumped nests) from evolving in breeding birds or creating songbird nesting patterns that simply are not detectable at the community level. Nonetheless, additional factors such as overlap of nest placement with predator territories (Erikstad *et al.* 1982, Sullivan and Dinsmore 1990) and search radius of predators relative to inter-nest distance (Andrén 1991) may have been influential in masking songbird nest spacing patterns.

Dispersion of songbird nests is generally attributed to results of competition among species and individuals for resources like food and space (Krebs 1971, Kaufman 1983, Armstrong 1991, Tye 1992). Although it has been hypothesized that spacing of nests through territoriality may be an anti-predator strategy, I found no evidence that predators

depredated more clumped versus randomly distributed songbird nests. However, it is still possible that predators influence songbird nesting patterns by forcing songbirds to select uniform distributions of nests because, in other studies, clumped artificial nests tended to suffer higher rates of predation than regularly dispersed nests (Picman 1988, Major *et al.* 1994). Nonetheless, most songbirds tend to nest in semi-clumped or semi-random patterns (Rothstein 1971, Harrison 1975, Lent and Capen 1995, Mönkkönen *et al.* 1996). Absence of nearest-neighbor effects for randomly distributed nests was consistent with some previous studies of natural nests (Blancher and Robertson 1985, Galbraith 1988, Andrén 1991, Schieck and Hannon 1993).

My findings suggest that nesting near neighbors may not be a disadvantage nor beneficial to songbirds breeding in early successional stages of mixedwood boreal forest. Clumping of avian nests is generally ascribed to communal nest defense of non-passerines that live in colonies (Göransson *et al.* 1975, Page *et al.* 1983, Niemuth and Boyce 1995, Berg 1996). However, clumped territories of warblers and swallows can maximize reproductive success in polygynous species and enhance foraging efficiency (Herremans 1993, Meek and Barclay 1996). Songbirds that have relatively weak defense mechanisms against predators (Morton *et al.* 1993, Sealy 1994) may actually benefit from vigilance and alarm calls from con- and hetero-specifics (Hogstad 1995, Forsman *et al.* 1998).

Detecting patterns of songbird species coexistence that are promoted by predators in boreal forest is immensely complicated by variability in predator communities and vegetation attributes. Future research must attempt to control these confounding factors via manipulative experiments to elucidate patterns and unravel potential underlying processes. Artificial nests have provided a relatively simple tool for researchers to explore whether predation is a process driving patterns of songbird species coexistence. Nonetheless, due to limitations of this approach (see Major and Kendal 1996), results should potentially be considered exploratory and used as a guide to develop more realistic tests of the predation hypothesis. Experimental manipulations of the predator community (e.g., additions, removals) are alternative approaches that could create variation in the abundance of one or multiple predator species across several seral

stages, controlling for the structure of the predator community as well as forest complexity associated with stand-age. Alternatively, point counts could be conducted in a large number of habitat types to capture wide-ranging variation in songbird and predator diversity. Controlling for vegetation, the predicted positive response of songbird diversity to predator diversity could be investigated. Lastly, work that examines the structure of predator communities and predator behavior as it relates to nest predation is urgently needed (Bayne and Hobson 1998, Söderström *et al.* 1998, Pelech 1999).

3.4.3 Conclusions

Contrary to predictions, artificial songbird nests deployed to simulate low similarity of breeding birds did not survive better than those mimicking high similarity. In the first experiment, predation of artificial nests did not increase as variance in vegetation at nest sites decreased across nest predation plots. Likewise, as predation increased across plots, variance among plots in nest-site vegetation at surviving nests did not increase. In the second experiment, predators did not respond differently to two-species versus three-species assemblages, except when nests destroyed by mice were considered survivors. These results suggest that predation was not a strong selective force in the partitioning of nest space, leading to coexistence of additional dissimilar species, and subsequently more diverse songbird communities. Although over-dispersion of nests is expected to be the best strategy for songbirds with weak mechanisms of nest defense, predators did not exert more intense selection on clumped versus randomly distributed nests. Hence, other biological, physical, and historical factors likely play more important roles in structuring songbird communities relative to predation, synergism among factors may swamp predator effects, or different predator species exert opposing forces of selection on nest-site partitioning, masking patterns at the community level. In particular, the importance of mice as nest predators and abilities of parent birds to defend nests against mice need further investigation. Overall, more experimentation is required to elucidate and fully understand the role predation plays in structuring songbird communities, through the use of artificial nests, but also the identification and manipulation of

predator communities in association with natural communities of breeding songbirds.

4. INFLUENCE OF NEST-SITE VEGETATION AND PREDATOR COMMUNITY ON THE SUCCESS OF ARTIFICIAL SONGBIRD NESTS

4.1 INTRODUCTION

Habitat selection involves discrimination among alternative habitats and may be affected by factors such as vegetation structure and floristics, presence of predators, food availability, presence of competitors, climate, and phylogenetic constraints (Cody 1985, Martin 1993a). These abiotic and biotic factors presumably can result in variation in the structure of avian communities, when they affect avian fitness. Predation is commonly the principal cause of nest mortality and some evidence suggests that predators can influence songbird habitat selection and partitioning of nest sites among species with similar nest-site characteristics (Martin 1988b, 1993a; Morton *et al.* 1993).

Several hypotheses have been advanced that link aspects of vegetation surrounding nests and nesting success (Martin 1988a, Steele 1993). Martin (1993a) postulated that dense foliage at nest sites may impede the transmission of sensory cues to predators or, alternatively, that the number of potential prey sites within a nest patch may affect predator searching efficiency. Nest concealment may be a key factor influencing reproductive success, although the relationship between concealment and nest losses is not consistent (Normant 1993, With 1994, Howlett and Stutchbury 1996). The susceptibility to predation of ground versus above-ground nests is also controversial; the relationship between concealment and nest height varies across habitats (Martin 1993b). These inconsistencies might be partially attributed to the nature of local predator communities. In particular, factors influencing nest success may vary depending on whether predator communities are dominated by mammals or birds, or whether visual or olfactory cues are used by predators to find nests (Whelan *et al.* 1994).

Identification of nest predators is necessary to assess critically results obtained from experiments evaluating success of artificial nests. However, the identity of predators

that remove eggs from artificial nests is often difficult to ascertain, despite innovative techniques such as plasticine eggs, cameras, hair-catchers, grease boards, and analysis of egg remains (Major and Kendal 1996, Marini and Melo 1998).

Most studies have compared vegetation characteristics at successful versus failed nests and artificial versus natural nests (Rudnicki and Hunter 1993, Wilson *et al.* 1998), but, to my knowledge, few studies have identified vegetation characteristics at nests depredated by specific types of predators. Examination of vegetation attributes that contribute to predator-specific nest losses yields a more comprehensive understanding of ecologically relevant factors that influence the choice of nesting habitats in birds and provides a foundation for land management decisions (Martin 1992, Steele 1993). I identified predators at artificial songbird nests and hypothesized that predation by different predator groups would vary with vegetation characteristics at nests.

4.2 STUDY AREA AND METHODS

Study plots (logged 1970 to 73) were located in mixedwood forest stands of the (Boreal) Lower Foothills Natural Region of Alberta (53°48'N, 116°14'W), dominated by trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), fir (*Abies* spp.), and balsam poplar (*Populus balsamifera*) comprised most of the remaining canopy. The understory was characterized, in decreasing importance, by willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), low-bush cranberry (*Viburnum edule*), *Ribes* (spp.), and wild rose (*Rosa* spp.).

In 1995 and 1996, experimentally comparable replicate plots were chosen to evaluate vegetation features associated with specific types of nest predators. All plots used the same experimental protocol, were established in the same habitat type, and contained wicker nests that varied only in nest-site vegetation and positioning of nests above ground. Plots (100 m x 100 m) were at least 800 m apart within years and 400 m apart between years. In 1995, 275 nests were deployed on 11 plots over a 4-day interval (17 to 20 June). Six of these plots had nests distributed on the ground and five plots had nests randomly distributed among five 1-m height classes ranging from 0-5 m. In 1996,

200 nests were deployed, 20 on each of 10 plots over a 6- or 3-day interval (2 to 7 June or 2 to 4 July). Five plots had nests deployed on the ground and five plots had nests randomly deployed in 1 of five 1-m height classes ranging from 0.5-5.5 m. On each plot, nests were randomly assigned to grid coordinates (10 m x 10 m) and deployed in locations typical of songbirds nesting in my study area. Nests were marked 2 m on either side by flagging tape of the same color as grid coordinate markers to prevent predators from cueing on nest sites.

Commercial wicker nests (10 cm outside diameter and 6 cm deep) were dipped in mud, air-dried, and lined with dry grass one week prior to use. Nests were baited with one Japanese quail (*Coturnix japonica*) and one plasticine egg painted to resemble a quail egg. Quail eggs were washed with tap water to remove odors prior to use. Above-ground nests were attached to nest substrates using clear monofilament line. Rims of ground nests were placed flush with the ground. Rubber gloves and boots were worn during nest deployment and checks (Rudnicki and Hunter 1993).

Predation rates on nests were measured by examining loss of eggs from nests every 3-5 days during a 12- or 15-day exposure period to predators. A predation event was recorded if any egg was penetrated or missing, or if a plasticine egg was marked. Predators were identified by noting triangular bill marks and measuring incisor widths in plasticine eggs. Incisor width and length measurements from 20 museum skulls of red squirrels (*Tamiasciurus hudsonicus*), red-backed voles (*Clethrionomys gapperi*), and deer mice (*Peromyscus maniculatus*) were used to categorize predators of plasticine eggs as avian, mouse, squirrel, and other mammals (Bayne 1996). Approximately equal numbers of male and female specimens were used.

Vegetation characteristics at nest sites were recorded at the end of experiments, when most vegetation growth was completed and little decomposition had started (15 June to 30 August). Point-quarter sampling was used to obtain tree (> 3 m tall) and shrub (> 1 m tall) measurements at nest sites (Krebs 1989). The area around each ground nest or the nest substrate stem at the base of an above-ground nest was divided into four equal quadrants and distances to the nearest tree and nearest green alder or willow were measured in each of the four quadrants. Tree and shrub density calculations

followed Krebs (1989). Plant species and height were recorded for the nearest tree and shrub in each quadrant (trees ± 0.5 m; shrubs ± 0.1 m). Relative abundance of coniferous versus deciduous trees and green alder versus willow were calculated based on the frequency of species in the four quadrants. Deciduous and coniferous trees (≤ 3 m) were counted in a 3-m radius circle around nests. Percent cover of bare ground and rock, ferns, grass/sedge, herbs, lichen, litter, moss, shrubs (< 1 m), water, and woody debris was estimated visually in a 2-m radius circle surrounding nests. Horizontal and vertical concealment of nests were estimated visually 1 m from nests in the four cardinal directions as well as 1 m above and below nests (for above-ground nests only). These estimates were averaged to obtain a single percentage value of a nest obscured by foliage. Tree and shrub closure was measured using a concave spherical densiometer held 110 cm above ground (Lemmon 1956). Six observers collected vegetation data over two years with individual observers collecting data in an equal number of plots each year. Consistency of visual estimations among investigators was checked prior to collecting these data.

Canonical variates analysis (CVA; Kshirsagar 1972) was used to determine differences in vegetation among 1) surviving nests; 2) nests depredated by mice (i.e., mice, voles), squirrels, and birds; and, 3) nests that had eggs removed by unidentified predators. To obtain reasonable levels of stability in canonical variate loadings and to ensure sample sizes within a group exceeded the number of variables by a factor of at least 3 (Williams and Titus 1988), Pearson product-moment correlations were used to delete intercorrelated vegetation variables ($r \geq 0.3$, $P \leq 0.0001$). For consistency, the strength of these correlation values and those relating canonical variate scores with original variables were considered moderate at 0.3-0.5 and strong at >0.5 . The 10 of 22 vegetation characteristics that remained after excluding correlated variables were considered to be biologically interpretable. I was also conservative by using total structure coefficients rather than individual coefficients to interpret the relative importance of each variable in distinguishing between successful nests and those depredated by different predator groups (Williams 1983). These two steps reduced the likelihood of obtaining unstable canonical coefficients from intercorrelated vegetation

variables. Wilks' Lambda test (Kshirsagar 1972) was used to determine if centroids of each group were significantly different.

Analyses of variance were used to test the relative importance of each vegetation variable separately. Variables that were proportions were arcsine transformed, while remaining variables were log transformed to improve normality. Statistical tests were conducted using SAS (1990).

4.3 RESULTS

Of 475 plasticine eggs, fate was unknown for 2% due to investigator bias or nest disturbance, 40% were in successful nests, and 20% were removed completely from nests by unidentified predators. The remainder of eggs were depredated by mice (14%), birds (12%), squirrels (6%), more than one predator type (3%), and large mammals (3%). Large mammals were those larger than squirrels. Because the CVA was conducted on only successful nests, nests missing eggs, and nests depredated by mice, birds, and squirrels, the total number of nests analyzed was 435.

Vegetation characteristics of successful nests overlapped with nests visited by all predator groups along CAN1, which explained 90% of the variance among nest categories (Fig. 4.1: Wilks' Lambda = 0.59, $F = 5.9$, $df = 40$ and 1598, $P = 0.0001$). When only ground nests were analyzed, patterns among successful nests and predator-specific nest losses were similar to those in Figure 4.1, except that birds only depredated nine ground nests. The distribution of successful nests most closely resembled the distribution of nests depredated by mice. The distribution of unidentified predators that removed eggs appeared bimodal, overlapping nests visited by squirrels and birds (Fig. 4.1).

Each type of predator visited nests with distinguishing vegetation features. Mice destroyed ground nests that were well concealed by shrubs (Table 4.1). Conversely, squirrels, birds, and unidentified predators removed eggs from poorly concealed above-ground nests. Nonetheless, these nests were in thickly wooded areas where there were few deciduous trees. The higher above ground a nest was placed, the greater the likelihood of being depredated by birds, squirrels, and mice, in that order. Fifty-six

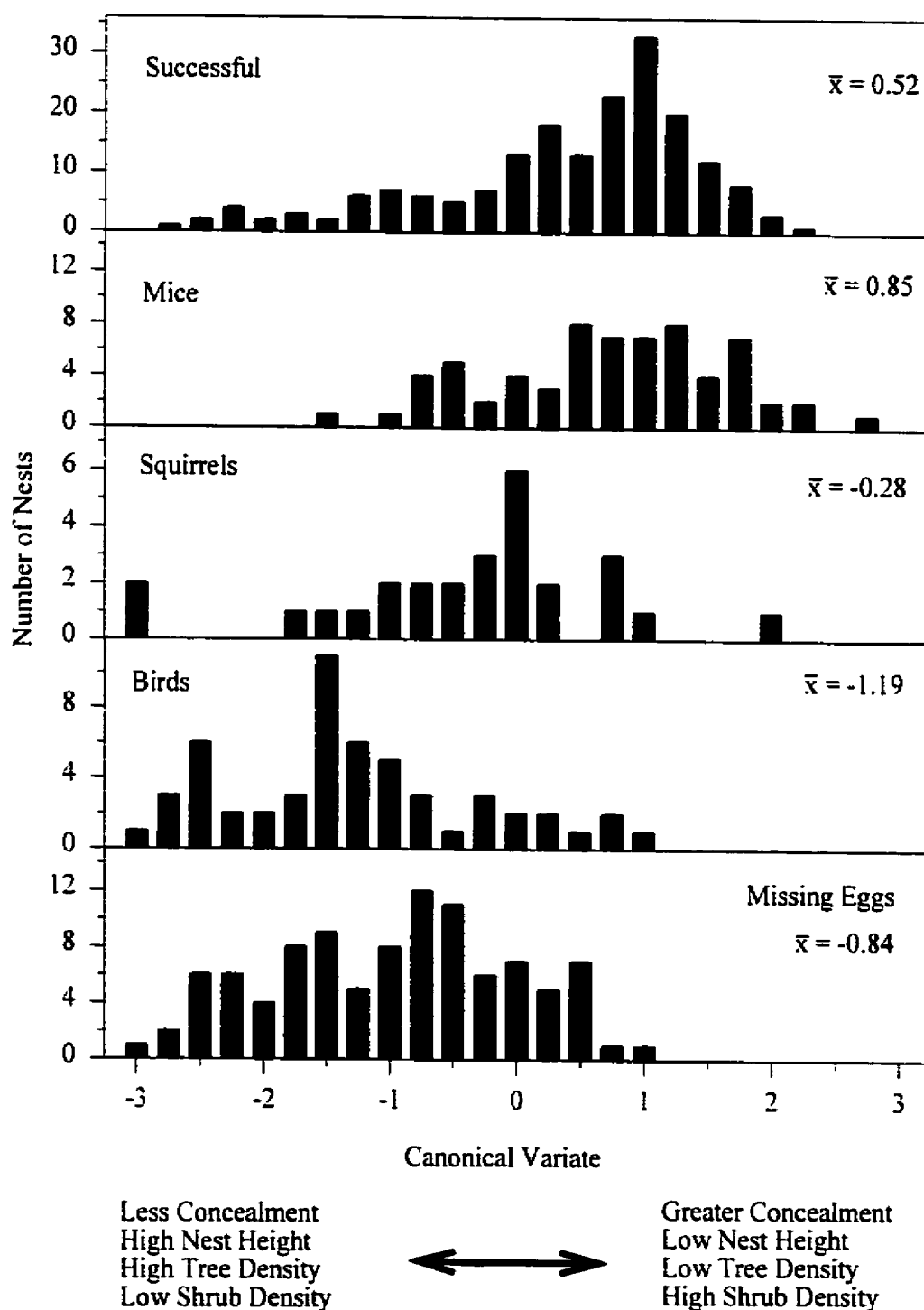


Figure 4.1. Frequency histograms of scores from the first canonical variate for successful nests ($n = 189$) and nests depredated by mice ($n = 67$), squirrels ($n = 27$), birds ($n = 55$), and unidentified predators that removed eggs from nests ($n = 97$) in boreal mixedwood forest stands in west-central Alberta (1995 to 1996).

Table 4.1. Vegetation attributes (mean \pm SE) for successful artificial nests ($n = 189$) and those depredated by mice ($n = 67$), squirrels ($n = 27$), birds ($n = 55$), and unidentified predators that removed eggs from nests ($n = 97$) in boreal mixedwood forest in west-central Alberta (1995 to 1996).

Vegetation attribute ^a	Successful nests	Nests depredated by				F^b	CAN1 ^c
		Mice	Squirrels	Birds	Unidentified predators		
Concealment (%)	66 \pm 1	66 \pm 2	61 \pm 4	46 \pm 3	53 \pm 2	16.2***	0.58
Nest height (m)	1.7 \pm 0.2	1.4 \pm 0.1	2.5 \pm 0.4	3.5 \pm 0.2	3.2 \pm 0.2	34.7***	-0.81
Tree density (/ha)	1857 \pm 398	1593 \pm 390	2226 \pm 495	6025 \pm 1071	3344 \pm 613	12.2***	-0.51
Tree height (m)	6.2 \pm 0.1	6.7 \pm 0.2	6.7 \pm 0.3	6.2 \pm 0.2	6.2 \pm 0.1	1.7	0.05
Coniferous trees (%)	7 \pm 0.5	8 \pm 1	6 \pm 0.1	5 \pm 0.6	5 \pm 0.4	2.0	0.19
Deciduous trees (%)	5 \pm 0.4	6 \pm 1	5 \pm 1	4 \pm 0.6	4 \pm 0.4	3.1*	0.27
Shrub density (/ha)	1428 \pm 192	2205 \pm 691	1084 \pm 294	617 \pm 202	787 \pm 111	9.7***	0.46
Green alder (%)	41 \pm 3	37 \pm 5	33 \pm 7	29 \pm 5	30 \pm 4	1.8	0.20
Shrub (%)	22 \pm 1	25 \pm 2	23 \pm 2	21 \pm 2	20 \pm 1	1.9	0.18
Woody debris (%)	3 \pm 0.3	3 \pm 0.4	3 \pm 0.8	3 \pm 0.5	3 \pm 0.4	0.6	0.08

^a Percentage values represent relative frequencies.

^b F -statistic from Analysis of Variance for differences among nest fate categories, * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$.

^c Correlations (r) between vegetation attributes and the first canonical variate (CAN1) are shown with moderate to strong correlations (≥ 0.30) presented in bold.

percent of nests depredated by squirrels were on the ground, compared with only 16% of nests depredated by birds.

Several vegetation variables were associated with CANI. Concealment and shrub density were positively correlated, whereas nest height and tree density were negatively correlated with CANI scores. These variables, in addition to the proportion of deciduous trees, also differed among groups of successful and failed nests when univariate tests were used.

4.4 DISCUSSION

4.4.1 Nest-Site Characteristics And Predator-Specific Nest Loss

Surviving nests and nests visited by mice were well concealed, similar to findings of studies involving natural nests (Murray *et al.* 1983, With 1994). Mice may be less affected by dense foliage surrounding nests because they are nocturnal mammals that use olfactory cues to forage and use dense foliage for foraging and protection from predators (Howard *et al.* 1968, Dooley and Bowers 1996). Successful nests and those depredated by mice were close to the ground, corresponding with the trend for higher predation rates on above-ground natural nests, though several studies have documented the reverse or no trend (Wilcove 1985, Morton *et al.* 1993, Wada 1994). Mouse predation was also linked to low tree densities, low litter accumulations, and high shrub densities, corresponding to habitat used by mice in artificial nest and population studies (Leimgruber *et al.* 1994, Carey and Johnson 1995). In contrast to results from other studies (Drickamer 1990, Bayne and Hobson 1997), I found that mice did not depredate nests in areas with high amounts of woody debris (Table 4.1), which provide nesting and protective cover, substrates for fungal sources of food, and travel lanes (Getz 1968, Wolff and Hurlbutt 1982, Barnum *et al.* 1992).

If vegetation characteristics related to the success of artificial nests are also similar for natural songbird nests that survive and nests destroyed by mice, then songbirds may be better able to defend their nests against mice. Conceivably, mice may be equally abundant at nest sites around surviving as failed nests, and the number of attacks on surviving nests may be comparable to the number of those on failed nests. However,

attacks on surviving nests may be thwarted by adults whose patterns of nest attentiveness coincide with nocturnal movements of mice and whose nest defence may be more successful against mice than larger-bodied predators (Verbeek 1970; Morton and Pereyra 1985). This emphasizes the need for research on nest defense by songbirds against mice because results of artificial nest studies, including mine, overlook the absence of vigilant parents.

Vegetation features at nests where eggs were missing were similar to those at nests depredated by squirrels and birds, strongly implicating squirrels and jays in the removal of eggs from nests. These findings were corroborated by the results of other studies in which squirrels and birds were observed removing eggs from nests (Sealy 1994; Bayne and Hobson 1999). Overall, vegetation characteristics at nests destroyed by squirrels, birds, and predators that removed eggs from nests were related to increased nest visibility. Predation rates commonly increase when nest or egg visibility increases or cover decreases at nests or nest patches, though there are many notable exceptions to this trend (With 1994; Howlett and Stutchbury 1996; Braden *et al.* 1997). Loss of poorly concealed nests suggests that squirrels rely on visual cues to detect prey, as is often the case for birds (Bayne and Hobson 1999). Red squirrels spend about 50% of their time mid-summer foraging on the ground, which likely increases their detection of nests located in sparse ground cover under a coniferous canopy (Benhamou 1996). With increased nest visibility, or conversely, decreased vegetation cover, the scent of humans or plasticine eggs may also have been more easily detected by predators, though research on squirrel and bird responses to nest odors is lacking (Whelan *et al.* 1994; Bayne and Hobson 1999).

My results indicated that, for mice, forest structure was more critical than floristics in determining the susceptibility of nests to squirrels and birds. Nest predation by squirrels and birds increased with greater tree density and lower shrub density, a pattern similar to some previous findings (Seitz and Zegers 1993). My results differ from some other studies that revealed more coniferous trees or fewer deciduous trees as primary vegetation features influencing nest predation; my plots were in mixedwood rather than pure coniferous or deciduous stands (Rudnicki and Hunter 1993; Huhta *et al.* 1996;

Bayne *et al.* 1997). Fewer shrubs at failed nests suggests that movements of squirrels and birds may be hampered by dense vegetation, or that nests were made more vulnerable when low shrub densities reduced the number of potential nest sites requiring searching (Bowman and Harris 1980; Martin 1993a).

4.4.2 Conclusions

Previous studies examined correlations between nesting success and habitat characteristics but not whether and how patterns of nest success vary with different nest predators. Furthermore, an ability to identify predators at natural nests has been often limited. Although there are limitations to artificial nest studies (see Major and Kendal 1996), my study provides an additional step in understanding habitat selection of forest songbirds, owing to links made between two cues in the environment, vegetation and nest predators. My study revealed that mice residing in dense foliage destroy well-concealed nests, implying that they counteract positive effects of nest concealment from other predators on reproductive success. 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 versus sustaining nest losses to mice (Martin 1988b), reinforcing the notion that birds face multiple selection pressures from the predator community. Moreover, above-ground nesting species, which may have less concealed nests than ground-nesting species in some forest types, may be trading-off concealment for better visual detection of encroaching squirrels and jays that are able to kill adults and destroy nest contents (Götmark *et al.* 1995). Ultimately, an understanding of how each predator species influences habitat-specific reproductive success will provide insight into ecological and evolutionary processes that shape habitat selection and life-history traits.

5. VISUAL AND OLFACTORY ATTRIBUTES OF ARTIFICIAL SONGBIRD NESTS

5.1 INTRODUCTION

Competition arising from food limitation has been considered a key influence affecting the organization of avian communities (Cody 1974; Martin 1986, 1987b, 1991). More recently, research has focused on predation as a process determining community structure (Martin 1988a,b, 1993a), particularly because predation is the primary cause of avian nesting mortality (Ricklefs 1969, Slagsvold 1982). Artificial nests have often been used as a surrogate for natural nests to elucidate patterns of nest predation across habitat types, season, nest types, and egg types (Møller 1987, Gibbs 1991, Götmark 1992a, Seitz and Zegers 1993, Andrén 1995), and, ultimately, to understand processes that shape life history traits, habitat selection, and community patterns (Martin 1987a). Artificial nest studies have also been used to investigate causes of purported declines of North American songbirds (Rappole and McDonald 1994, Sauer *et al.* 1996) and to provide management recommendations for mitigating losses to predators (Wilcove 1985, Huhta *et al.* 1996, Ammon and Stacey 1997).

Artificial nests can facilitate controlled experiments with strong statistical designs (Reitsma *et al.* 1990), but these experiments often assume that predators search for and respond to artificial nests in the same way that they do natural nests (Martin 1987a). Some studies have found no difference in nesting success for artificial and natural nests (Gottfried and Thompson 1978, Andrén *et al.* 1985, Butler and Rotella 1998), whereas others have found success of artificial nests to be lower than natural nests (MacIvor *et al.* 1990, Ammon and Stacey 1997, Ortega *et al.* 1998, Wilson *et al.* 1998) or vice versa (George 1987, Storaas 1988, Roper 1992, Guyn and Clark 1997).

Predation of artificial nests may not be comparable to that on natural nests because of the appearance of artificial nests (see Major and Kendal 1996). Conspicuousness of

songbird nests varies with nest height and substrate (Ricklefs 1969, Martin 1993b, Wada 1994, Howlett and Stutchbury 1996). Songbirds that build open-cup nests may minimize nest detection by predators by using materials that visually blend into the site surrounding a nest or create textured appearances (Harrison 1975, Erhlich *et al.* 1988). Unmodified wicker nests used in artificial nest studies may be conspicuous (Wilcove 1985, Reitsma *et al.* 1990, Gibbs 1991; but see Martin 1987a). Some experimenters dip nests in mud to modify their stark appearance (Cotterill 1996), but artificial nest silhouettes nonetheless may be more distinct than those of natural nests.

Odors of humans, dummy eggs, and nest material may be present at artificial nests (Hoi and Winkler 1994, Whelan *et al.* 1994). In contrast, odors of adult birds and natural nests and eggs are absent (Møller 1987, Götmark 1992b). Odors emanating from bird nests can either increase (Swennen 1968, Green and Anthony 1989) or decrease (Petit *et al.* 1989, Whelan *et al.* 1994, Clark and Wobeser 1997) clutch survival. Nocturnal mammals tend to respond more than birds to odors at natural and artificial ground nests (Storaas 1988, Petit *et al.* 1989, Bayne *et al.* 1997). Recent studies have used plasticine eggs to identify predators (Willebrand and Marcström 1988, Ammon and Stacey 1997, Hannon and Cotterill 1998); yet, the unnatural odor of plasticine may attract predators and inflate predation rates. Unusual odors due to egg age may also confound artificial nest studies (Major 1991), but this has rarely been tested (Henry 1969, Whelan *et al.* 1994).

Egg size and shell thickness may complicate the use of quail eggs (Roper 1992, DeGraaf and Maier 1996, Marini and Melo 1998). Predation by small mammals can be missed altogether when large quail eggs are used, leading to spurious conclusions for experimental treatments (Roper 1992; Haskell 1995a,b; Bayne *et al.* 1997). Documenting predation events that would otherwise be missed by using quail eggs can be achieved by using plasticine eggs (Major *et al.* 1994, Bayne *et al.* 1997, Darveau *et al.* 1997). Eggs of domestic finches that are of similar size and strength as natural songbird eggs, however, may result in more realistic predator responses than either quail or plasticine eggs, but to my knowledge this possibility has not been evaluated.

Using field and laboratory experiments, I investigated the response of predators to

variation in artificial nest appearance and to presence of quail, finch, and plasticine eggs. Because diurnal predators, particularly birds, rely heavily on visual cues (Howlett and Stutchbury 1996), I predicted that avian predators would find more wicker nests dipped in mud than wicker nests covered by a camouflage fabric. Due to the odor of plasticine eggs, artificial nests or egg assortments offered to nocturnal mammals containing plasticine eggs should suffer higher rates of predation than nests or egg assortments containing only finch and quail eggs. Mice and voles (hereafter, mice refers to both mice and voles) are typically unable to break quail eggs and use olfaction to detect food. Thus, I predicted that these predators would depredate a greater proportion of plasticine than finch and quail eggs and a greater proportion of finch than quail eggs in field and laboratory experiments.

5.2 STUDY AREA AND METHODS

Field sites were located in boreal mixedwood forest stands (14 to 60 ha) in west-central Alberta (53°48'N, 116°14'W) that were logged in 1970 to 72 (elevation 1,060 to 1,170 m). The study area was highly fragmented by logging and oil and gas exploration, and stands were at least 60 km from the nearest human population ($\geq 10,000$ people). Within constraints of stand size, experimental plots were placed at least 50 m from stand edges that were often bordered by logging roads.

Stands were dominated by trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), fir (*Abies* spp.), and balsam poplar (*Populus balsamifera*) comprised most of the remaining canopy. The understory was characterized, in decreasing importance, by willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), cranberry (*Viburnum edule*), *Ribes* species, and wild rose (*Rosa* spp.).

Potential mammalian predators in the study area included red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys gapperi*), western jumping mice (*Zapus princeps*), least chipmunks (*Eutamias minimus*), alpine chipmunks (*Eutamias alpinus*), black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), coyotes

(*Canis latrans*), pine martens (*Martes martes*), fishers (*Martes pennati*), least weasels (*Mustela nivalis*), long-tailed weasels (*Mustela frenata*), and short-tail weasels (*Mustela erminea*). Potential avian predators included Common Ravens (*Corvus corax*) and Gray Jays (*Perisoreus canadensis*).

5.2.1 Predator Response To Nest Appearance

I modified half of my commercial wicker nests (10 cm outside diameter and 6 cm deep) by sewing camouflage cloth to the outer surface and over the rim of nest bowls to break up the outline of nests and to better mimic the mottled appearance of natural nests. The pattern and colors of the material blended with the bark and foliage of deciduous and coniferous trees in my area. I modified the remaining nests by dipping them in mud to reduce their brightness (hereafter, mud nests; Cotterill 1996). All nests were aired and lined with dry grass one week prior to use.

Five forest stands were selected and in each I established paired 1-haplots 100 m apart. Nest types (i.e., camouflage and mud) were randomly allocated to these paired plots. Twenty nests were deployed (2 to 7 June 1996) in each plot at random coordinates, using a 10 x 10 m grid scale, with the condition that nests were placed where songbirds in my area would be expected to nest (20 nests/ha). Nests were randomly, yet evenly distributed, among five 1-m height classes ranging from 0.5 to 5.5 m. All nests were attached to substrates using monofilament line. Rubber gloves and boots were worn during nest deployment and checks (Rudnický and Hunter 1993). One Japanese Quail (*Coturnix japonica*) egg and one plasticine egg, painted to resemble a quail egg, were placed in each nest. Nests were checked every five days over a 15-day period. A predation event was recorded if any egg was penetrated or missing, or if a plasticine egg was marked. Penetrated eggs were classified as either punctured, cracked, or broken.

Vegetation characteristics at nest sites were recorded at the end of the experiment. Plants were designated as trees or shrubs using taxonomy. Large tree (> 3 m tall) and large shrub (\geq 1 m tall) measurements were obtained at nest sites using point-quarter sampling (Krebs 1989). The area around each ground nest or the nest substrate stem at

the base of an above-ground nest was divided into four equal quadrants and distances to the nearest tree and nearest green alder or willow were measured in each quadrant. Calculations of tree and shrub densities followed Krebs (1989). Plant species and height were identified and measured, respectively, for the nearest tree and shrub in each quadrant (trees ± 0.5 m; shrubs ± 0.1 m). Relative abundance of coniferous versus deciduous trees and green alder versus willow were calculated based on the frequency of species in the four quadrants. Small deciduous and coniferous trees (≤ 3 m) were counted in a 3-m radius circle around nests. Percent ground cover of bare ground and rock, ferns, grass/sedge, herbs, lichen, litter, moss, shrubs (< 1 m), water, and woody debris was estimated visually in a 2-m radius circle surrounding nests. Heights of nest substrates were recorded. Horizontal and vertical concealment of nests were estimated visually 1 m from nests in the four cardinal directions as well as 1 m above and below nests. These estimates were averaged to obtain a single percentage value of a nest obscured by foliage. Tree and shrub closure was measured using a concave spherical densiometer held 110 cm above ground (Lemmon 1956). Five observers collected vegetation data with observers measuring characteristics at an equal number of mud and camouflage nest sites. Visual estimations among investigators were calibrated prior to collecting these data.

5.2.2 Predator Response To Nest Contents

In each of eight forest stands, independent of the nest appearance experiment, nests were deployed (5 to 13 July 1997) at two locations (100 to 275 m apart), each containing three parallel transects (320 m long). Nests within stands were placed at least 800 m from those in replicate stands. At 40 m intervals along the three transect lines, single stations were erected across transects, totaling eight stations per location. Thus, each station contained three nests, one on each transect (25 m apart). Three egg treatments were randomly assigned to the three nest sites at each station for a total of 384 nests (3 nests \times 8 stations \times 2 locations \times 8 stands) and densities of 15 nests/ha. Pairing treatments at stations helped control for local vegetation effects. Nests had rims of nest bowls flush with the ground.

Wicker nests (9.5 cm outside diameter and 3.8 cm deep) were baited with (1) one quail and one finch ($n = 128$ nests); (2) one quail, one finch, and one plasticine ($n = 128$ nests); and, (3) one quail, one finch, and five plasticine eggs ($n = 128$ nests). Finch eggs were included in each nest to evaluate the importance of small rodents as predators of eggs. Quail and finch eggs were washed with tap water prior to use to remove odors and were visually inspected for cracks and punctures immediately before placement into nests. Finch eggs, obtained from hobby breeders in Canada and the United States, were refrigerated for up to two months before deployment in the field and were not refrigerated for \leq seven days during transit to the study area. Finch eggs were used from Society Finch (*Lonchura domestica*), Gouldian Finch (*C'hoebia gouldiae*), and Red-cheeked Finch (*Uraeginthus bengalus*), though the color and size of these eggs were similar. Plasticine eggs simulated the size, shape, and color of white finch eggs and did not require painting.

Predation rates on artificial nests were measured by examining loss of eggs from nests every four days during 12 days of exposure to predators. Nests containing only quail and finch eggs were considered destroyed by mice when (1) eggs were damaged and mouse scats were present at a nest; (2) finch eggs were damaged but quail eggs were intact; and, (3) intact finch eggs had small incisor marks. All surviving finch eggs were opened, at the end of the experiment, to determine their state of deterioration. Concealment was measured at all nests as in the previous experiment.

5.2.3 Response Of Captive Deer Mice To Plasticine Eggs

To complement results of my field experiment, I offered wild deer mice assortments of eggs under controlled conditions (Canadian Council on Animal Care Protocol #940195). Mice were housed in shoe-box cages at room temperature and a natural photoperiod for at least 10 days prior to the experiment. Rodent chow was available *ad libitum* and was removed from cages 30 min before each trial. Forty mice (each used only once) were randomly given one of two egg assortments that had been used in the field: (1) one finch and one quail egg; and (2) one finch, one quail, and one plasticine egg. I reasoned that the use of fresh finch eggs would eliminate any

confounding effects that may have arisen from the use of old finch eggs in the field. Eggs were placed at random, 1 cm apart, in a row at the front of cages about 1 h after sunset. Mice were illuminated using an infrared lamp and were observed from behind a blind. The number of minutes to perform three foraging behaviors (touch with the nose, bite, and penetrate) was recorded for all eggs. Time zero was recorded when mice approached eggs if at least one egg was subsequently touched. Further contact with any egg could be interspersed with activities other than foraging (e.g., resting, grooming). From the time mice first approached eggs (and subsequently touched an egg), they were observed for 2.5 h.

5.2.4 Quail And Finch Eggshell Measurements

To obtain a relative index of the strength of finch and quail eggshells, eggs were depressed at the equator by a 2 mm probe advancing at a constant rate of 0.2 mm/s with a 2 kg load cell using a Food Texture Analyzer (Texture Technologies Corp. Model TA.XT2). The texture analyzer was set to penetrate a distance of 3 mm after a sensory trigger force of 1 g was detected upon contacting the egg. The software package XT.RA dimension V3.5 (Stable Micro Systems, Surrey, England) recorded the force (kg) of depression on the egg when it fractured.

Length (L) and breadth (B) of all eggs were measured with Vernier calipers to the nearest 0.01 mm and egg shape was determined by the ratio of L:B. Egg volume was calculated using the equation derived by Spaw and Rohwer (1987). Mean shell thickness (including membranes) was measured at three sites on egg equators with a micrometer (nearest 0.001 mm). Shells were oven dried at 50° C for 24 h prior to measurements.

5.2.5 Statistical Analyses

I used logistic regression (Manly *et al.* 1993) to examine effects of nest appearance and vegetation variables on nest fate. Two-way interactions with nest appearance were also investigated. To reduce multicollinearity, some vegetation variables that were highly correlated (Pearson product-moment correlation; $P \leq 0.01$) with other variables were deleted (e.g., retained variable = grass; deleted variables = litter, moss, woody

debris). The most parsimonious model was attained by sequentially deleting non-significant interactions and then main effects. To determine if nests containing plasticine eggs were more susceptible to predation, I compared the mean number of days nests survived ($n = 8$ stands) among egg treatments using a Jonckheere (J) test for ordered alternatives (Siegel and Castellan 1988). This analysis tested the alternative hypothesis that the median number of days nests survived was ordered in magnitude for egg treatments: five plasticine/one quail/one finch < one plasticine/one quail/one finch < one quail/one finch. Pairwise comparisons followed methods of Zar (1984). Logistic regression was used to examine the relationship between concealment and fate as well as concealment and egg treatment. For clarity, these tests are also referred to in the Results as well as commonly used parametric and nonparametric tests (Zar 1984). Statistical tests were conducted using SAS (1990).

5.3 RESULTS

5.3.1 Predator Response To Nest Appearance

Twenty-four percent of nests survived, 74% failed, and 2% were of unknown fate. Of depredated nests, 74% had both eggs destroyed and 26% had only one egg destroyed. Tooth and beak marks in plasticine eggs allowed predators to be identified at 49% of failed nests (birds 33%, squirrels 7%, small mammals 7%, mice 1%, large mammals 1%). The small mammal category includes mice and juvenile squirrels that could not be clearly differentiated. A significant difference occurred in the number of plasticine eggs destroyed by birds and small mammals as a function of nest appearance ($G = 4.6$, $df = 1$, $P = 0.03$). This difference was caused by birds destroying more mud (29 of 36 destroyed) than camouflaged nests (20 of 35). Small mammals tended to depredate more camouflaged (15 of 35) than mud nests (7 of 36).

Logistic regression was used to evaluate simultaneously whether nest fate was related to nest appearance (i.e., mud versus camouflage), nearest-neighbor distance, height class of nests, concealment, proportion of herbs, grass, coniferous trees, shrub density, proportion of willow, and number of coniferous trees ($n = 196$). When the model was reduced by eliminating non-significant interactions and then main effects (all

$X^2 < 2.0$, all $P > 0.15$), the probability of a nest being depredated was not related to nest appearance ($X^2 = 0.0$, $df = 1$, $P = 0.96$). Increased cover by grass ($X^2 = 5.5$, $df = 1$, $P = 0.02$) and overall concealment by vegetation ($X^2 = 7.5$, $df = 1$, $P = 0.01$) enhanced nest survival, whereas more willow ($X^2 = 4.6$, $df = 1$, $P = 0.03$) and coniferous trees (< 3 m tall; $X^2 = 6.1$, $df = 1$, $P = 0.01$) at nest sites lowered nest survival. The biological relevance of significant vegetation variables in the model is discussed elsewhere (Chapter 4, Rangen *et al.* 1999).

5.3.2 Predator Response To Nest Contents

Predators of plasticine eggs attacked 70.5% of deployed nests ($n = 384$). Mice destroyed the majority of plasticine eggs (59%) followed by unidentified predators (35%), small mammals (mice or squirrels: 3%), squirrels (2%), and mammals larger than squirrels (1%). The percentage of unidentified predators decreased 2-fold when one plasticine egg was used and decreased an additional 3-fold when five plasticine eggs were used. At nests visited by mice and unidentified predators, almost all quail eggs remained intact (Fisher's exact test; Table 5.1). In contrast, two-thirds of finch eggs remained intact (G -test; Table 5.1) and of those penetrated, 12% were cracked, 12% were broken, and 5% were punctured. Mice tended to leave finch eggs intact, whereas unidentified predators left similar numbers of intact and penetrated eggs. At the end of the experiment, 62% ($n = 151$) of finch eggs appeared to be at some stage of decay, 26% ($n = 64$) were relatively fresh, and 12% ($n = 30$) were desiccated. Scats of mice were found at some nests of each treatment, but finch and quail eggs were not always penetrated. Mice were more likely to leave plasticine eggs in nests ($n = 134$) than remove one or more of them ($n \leq 11$; $G = 88.5$, $df = 2$, $P = 0.001$), whereas unidentified predators were more likely to remove plasticine eggs from nests than leave them (remaining = 16; one removed = 29; > one removed = 15; $G = 15.7$, $df = 2$, $P = 0.001$). Of nests containing plasticine eggs that were depredated by mice, 3% had no plasticine eggs, 71% had one plasticine egg, and 26% had greater than one plasticine egg bitten ($G = 195.2$, $df = 2$, $P = 0.001$).

Contrary to results from the experiment on nest appearance, logistic regression

Table 5.1. Condition and number of finch and quail eggs in nests visited by mice and unidentified predators in boreal mixedwood forest stands in west-central Alberta (July 1997).

Predator	Finch ^a			Quail ^b		
	Intact	Penetrated	Missing	Intact	Penetrated	Missing
Mice ^c	128	27	6	158	3	0
Unidentified	36	44	14	80	8	6

^a $G = 44.3$, $df = 2$, $P = 0.001$.

^b Fisher's exact test; $P = 0.0001$.

^c Mice includes mice and voles.

indicated that nest failure was not related to concealment ($X^2 = 0.4$, $df = 1$, $P = 0.53$), and concealment did not vary with egg treatment ($X^2 = 1.2$, $df = 2$, $P = 0.55$). Predation rates were higher for nests containing plasticine eggs than quail and finch eggs only (median survival = 10.2 days, 6.8 ± 0.8 SE nests destroyed, $n = 8$ stands), though not between nests containing one (median survival = 5.8 days, 13.1 ± 1.0 nests destroyed, $n = 8$ stands) and five plasticine eggs (median survival = 5.4 days, 14.1 ± 0.5 nests destroyed, $n = 8$ stands; $J = 186$, $P = 0.005$). Similarly, the direction of the predicted order of predation was the same for all eight stands, with nests containing five plasticine eggs always having higher predation than nests containing one or no plasticine eggs, and nests containing one plasticine egg always having higher predation than nests containing no plasticine eggs. More finch ($n = 111$) than quail eggs ($n = 42$) were penetrated (McNemar tests: $X^2_c = 48.7$, $P = 0.001$), and more plasticine ($n = 196$) than finch eggs ($n = 61$) were penetrated ($X^2_c = 105.0$, $P = 0.001$) for one and five plasticine egg treatments combined (nests with five plasticine eggs only contributed one depredated plasticine egg to the sample size shown).

5.3.3 Response Of Captive Deer Mice To Plasticine Eggs

Mice took 12 times longer to bite eggs in assortments of only quail and finch eggs than in assortments that also contained plasticine eggs (t -tests: Table 5.2). Time to penetrate finch eggs in assortments of quail and finch eggs was 24 times longer than to penetrate eggs (finch or plasticine) in assortments that also contained plasticine eggs. An overall effect of plasticine eggs occurred for two-egg assortments when all three foraging behaviors were analyzed (MANOVA: Wilks' Lambda = 0.7, $F = 16.6$, $df = 3$ and 28, $P = 0.001$), but the tendency was weaker when touching and biting were evaluated alone (MANOVA: Wilks' Lambda = 0.9, $F = 3.2$, $df = 2$ and 36, $P = 0.06$).

Within finch and quail egg assortments, more quail ($n = 15$) than finch eggs ($n = 4$) were touched first (Chi-square: $X^2 = 6.4$, $df = 1$, $P = 0.01$) and, overall, quail eggs were touched in less time than were finch eggs (Table 5.3). However, finch eggs were bitten sooner (Chi-square: $X^2 = 12$, $df = 1$, $P = 0.001$) and had a greater number of eggs penetrated than quail eggs (12 versus 0).

Table 5.2. Time (min) taken (mean \pm 1 SE) by captive deer mice to touch, bite, and penetrate the first egg in assortments of finch and quail eggs versus assortments containing plasticine eggs. Significance (P) of t -tests are shown.

Foraging behavior	Egg assortment				P
	Finch and quail	n	Plasticine, finch, and quail	n	
Touch	0.88 \pm 0.23	19	0.55 \pm 0.15	20	0.22
Bite	10.59 \pm 6.41	19	0.88 \pm 0.21	21	0.03
Penetrate	40.30 \pm 12.83	12	1.67 \pm 0.44	20	0.002

Table 5.3. Time (min) for captive deer mice to sample plasticine, finch, and quail eggs offered as an assortment of finch and quail eggs versus plasticine, finch, and quail eggs. Shown are medians (range), number of captive deer mice (n), and P values.

Foraging behavior	Egg type						<i>P</i>
	Plasticine	<i>n</i>	Finch	<i>n</i>	Quail	<i>n</i>	
Finch and quail							
Touch	- ^a	-	0.7 (0.1-64.0)	19	0.5 (0.1-3.8)	19	0.001 ^b
Bite	-	-	1.6 (0.4-110.1)	17	2.7 (0.2-132.4)	19	0.001 ^b
Penetrate	-	-	18.4 (3.2-129.6)	12	-	0	-
Plasticine, finch, and quail							
Touch	0.8 (0.1-7.9)	20	0.8 (0.1-14.7)	20	0.6 (0.2-103.9)	20	0.89 ^c
Bite	0.9 (0.1-8.0)	20	1.3 (0.2-20.5)	19	2.1 (0.3-103.9)	19	0.16 ^c
Penetrate	0.9 (0.1-7.9)	20	4.7 (1.1-90.1)	14	-	0	0.002 ^b

^a Dashes indicate that plasticine eggs were not part of finch and quail egg assortments or no time to penetrate quail eggs was recorded.

^b Wilcoxon signed-rank test.

^c Kruskal-Wallis test.

Within plasticine, finch, and quail egg assortments, there was a tendency for more plasticine ($n = 11$) than quail ($n = 5$) or finch eggs ($n = 4$) to be bitten first (Chi-square; $X^2 = 4.3$, $df = 2$, $P = 0.12$). Nonetheless, more plasticine eggs were penetrated first (Chi-square; $X^2 = 16.2$, $df = 1$, $P = 0.001$) and plasticine eggs were penetrated in less time than finch eggs (Table 5.3). More plasticine eggs were punctured than the other two egg types (Cochran Q-tests; $Q = 24.6$, $df = 2$, $P = 0.001$) and more finch eggs were eaten than quail eggs ($Q = 57.4$, $df = 2$, $P = 0.001$). Plasticine eggs were touched, bitten, and penetrated all at once, whereas additional time was required for mice to penetrate finch eggs after touching them (Table 5.3).

Across assortments, most mice (93%, $n = 26$) broke into finch eggs at the small end of the egg while no quail eggs were broken. From the time mice approached eggs, they had a mean of 9.4 ± 0.8 SE contacts ($n = 40$) with quail eggs, each contact lasting 1 s to 5 min 46 s. Some mice were more aggressive in attempts to penetrate plasticine and quail eggs when a food reward had already been received from a finch egg. Time spent during a single contact with quail eggs generally attenuated during a trial. Mice sometimes leveraged quail eggs against their abdomen or sides of cages in attempts to open the eggs.

5.3.4 Quail And Finch Eggshell Measurements

Quail eggs had larger egg volumes (mean = 8.78 ± 0.14 cm³, $n = 52$) than finch eggs (mean = 1.17 ± 0.02 cm³; $n = 52$; $t = 52.7$, $P = 0.0001$). Quail eggshells were also 13 times stronger (mean = 1.21 ± 0.06 kg, $n = 26$ versus mean = 0.09 ± 0.004 kg, $n = 26$; $t = 17.3$, $P = 0.0001$) and three times thicker than finch eggs (mean = 0.25 ± 0.003 mm, $n = 52$ versus mean = 0.08 ± 0.005 mm, $n = 52$; $t = 30.7$, $P = 0.0001$). Finch eggs were more pyriform (mean = 1.33 ± 0.01 , $n = 52$) than quail eggs (mean = 1.25 ± 0.01 , $n = 52$; $t = -5.4$, $P = 0.0001$).

5.4 DISCUSSION

If results of artificial nest experiments are to contribute to an understanding of the evolutionary significance of predation in structuring bird communities or how habitat changes impact birds, then methodology of artificial nests must be critically assessed.

Many studies that use artificial nests have focused on the influence of habitat type, vegetation, spatial effects, nest density, and observer biases on nest predation (see Major and Kendal 1996). However, testing the reliability of experimental nests and egg types used in artificial nest studies is the first logical step required to improve our understanding of this experimental approach. Based on my results, simple modification of a wicker nest may not be adequate to simulate natural nests, yet choice of egg type appears critical in obtaining patterns of predation more closely resembling natural situations.

5.4.1 Nest Appearance

Physical characteristics of artificial nests, including lining, size, and type, can influence predation (Møller 1987, 1990; Gibbs 1991, Sieving 1992). However, I found no evidence that avian predators perceived camouflaged and mud nests differently; thus, both nest types may have been viewed merely as conspicuous, dense objects. Cresswell (1997) claimed that predation of natural nests deployed in an artificial nest study was independent of physical traits of nests but related to nest detectability and height. Nest visibility as it relates to concealment was important in explaining fate of my nests and visibility often is reported to influence nesting success (Yahner and Wright 1985, Norment 1993, Gregg *et al.* 1994, Clark and Shutler 1999). It is possible that the lack of a nest appearance effect was also related to predators increasing their foraging rate to compensate for prey that was more difficult to find (i.e., camouflage nest: Guilford and Dawkins 1987, Lawrence 1989, Krebs and Davies 1997) or forming search images for eggs rather than nests (Montevocchi 1976, Vacca and Handel 1988, Hoi and Winkler 1994, Yahner and Mahan 1996).

The tendency of small mammals to preferentially depredate camouflaged nests may be similar to previous studies where predators preferentially depredated natural and wicker nests modified to simulate nests of specific species versus unmodified wicker nests (Martin 1987a, Gibbs 1991). It may be argued that such results support the “search image” hypothesis (Martin 1987a) and that search images formed by predators for natural nests (or natural-looking artificial nests) are stronger than those formed for

wicker nests. Because small mammalian predators in my study do not rely solely on visual cues, attributes other than the appearance of wicker nests (e.g., dyes and volatile chemicals in the camouflage fabric) may influence predation risk. Nonetheless, further tests of the “search image” hypothesis (Guilford and Dawkins 1987) require that predators be identified as visually or olfactorily oriented.

5.4.2 Predator Response To Egg Type

I demonstrated that different egg types detect effects of different components of the predator community, which may explain some of the controversy in the literature. For example, higher predation rates have been documented for fragmented versus contiguous forest when only quail eggs were deployed (Wilcove 1985, Small and Hunter 1988, Burger *et al.* 1994). This may be due to preponderance of avian predators at edges, typically corvids (Andr  n 1992, 1995), that are capable of breaking quail eggs, but also to the inability to document predation by small mammals that prefer forest interior (Wauters *et al.* 1994, Mills 1995, Sekgororane and Dilworth 1995). Plasticine eggs, however, allow documentation of predation by these small mammals, resulting in similar rates of predation for the two forest types (Nour *et al.* 1993), or higher predation in contiguous versus fragmented forest (Haskell 1995b). Studies using plasticine eggs have reported higher predation rates for ground than above-ground nests (Bayne *et al.* 1997), although patterns of predation for ground and above-ground natural nests are also inconsistent (Martin 1993b, Wada 1994, Matsuoka *et al.* 1997b). Plasticine eggs, therefore, may record predation events from small ground-dwelling mammals that are attracted to artificial nests that would not otherwise visit natural nests.

My field and laboratory experiments corroborated findings of other studies that mice were unable to break quail eggs (Roper 1992, Haskell 1995a, Vander Haegen and DeGraaf 1996) and that quail eggs result in low predation (Nour *et al.* 1993, Bayne *et al.* 1997, Bayne and Hobson 1999). Quail eggs were simply too large for deer mice to grasp with their jaws and shells were stronger and thicker than those of domestic finch and songbirds (Picman *et al.* 1996, Spaw and Rohwer 1987). Some researchers have treated quail eggs with acetic acid to thin eggshells, and have assumed that treated eggs

can be penetrated by small mammals (Picman *et al.* 1993, Jobin and Picman 1997). Overall, if the species composition of small-gaped mammals in the predator community is not the same among experimental treatments, quail eggs may not provide a reliable index of relative predation rates (Roper 1992, Haskell 1995b). Nonetheless, quail eggs may still be useful if mostly large predators comprise the predator community (Arango-Vélez and Kattan 1997, Craig 1998).

Mice rely strongly on their sense of smell while foraging (Howard *et al.* 1968, Anderson 1986, Coulston *et al.* 1993). I found that predators, mostly mice, depredated more nests that contained plasticine eggs, and I suspect that plasticine odors were responsible. Plasticine may result in higher rates of predation by attracting predators and by having a soft material that is easily penetrated compared to quail and finch eggs. If mammals that use olfactory cues comprise a large portion of the predator community in one experimental treatment versus another (e.g., habitat type), differences in relative predation rates among experimental treatments may not be accurate. Predators preferred plasticine eggs even though finch eggs provided a food source; the same was observed with captive deer mice. However, the number of plasticine eggs in nests did not influence the probability that eggs would be bitten. Once bitten, the taste of a plasticine egg, or the lack of a food reward may have deterred small mammals from sampling other eggs. Results of another study suggested mice were attracted to plasticine because mice were not primary predators of natural Song Sparrow (*Melospiza melodia*) nests, but mice became key predators when these nests were relocated and baited with quail and plasticine eggs (Rogers *et al.* 1997). Their results, however, could also be an artifact of lack of parental activity at artificial nests (Verbeek 1970, Maxson and Oring 1978). Bayne and Hobson (1999) found that predators did not respond differently to quail eggs in artificial nests that had plasticine placed underneath versus nests only containing quail eggs. Owing to the size and strength of quail eggs, however, Bayne and Hobson (1999) essentially were examining the response of squirrels rather than mice to plasticine odors.

Captive deer mice were attracted to egg assortments containing plasticine, supporting results of the artificial nest experiment and further suggesting that predators

were not affected by the presence of old finch eggs (Whelan *et al.* 1994). If old finch eggs had initially attracted mice to nests rather than plasticine eggs, this may have explained why only one plasticine egg was bitten instead of five, but it does not explain why mice did not eat old finch eggs.

The lower number of finch versus plasticine eggs consumed in the wild may be related to egg condition for two reasons. First, small cracks and punctures in eggs may have provided sensory stimulation to animals sufficient to indicate that eggs were not highly palatable. However, cracked eggs can also increase the transmission of olfactory cues and increase predation (Olson and Rohwer 1998). Mice sometimes punctured eggs with their teeth at artificial nests, which also has been noted at natural nests (Maxson and Oring 1978). Thus, predator attacks that destroy eggs but does not lead to consumption may be typical in the wild. Second, handling times required by captive mice to break finch eggs were substantial (40 min and 15 min). It is not known how much time and energy predators allocate to breaking eggs in the wild, but deer mice and red-backed voles spent no more than 15 s at artificial nests containing quail eggs in medium-age hardwood forest in Minnesota (Fenske-Crawford and Niemi 1997). Lack of a food reward seems an unlikely explanation for the short time mice spent at nests because gray (*Sciurus carolinensis*) and red squirrels in aspen and pine dominated forests, that can break quail eggs, assessed nests for only 15 s and 42 s, respectively (Boag *et al.* 1984, Fenske-Crawford and Niemi 1997). Thus, foraging mice may investigate a potential food source, but if positive reinforcement is not obtained shortly thereafter, it may be advantageous for them to continue foraging elsewhere.

5.4.3 Conclusions

Sensory cues associated with artificial nests influenced rates of predation, emphasizing the need for investigators to match nest and egg models to predator communities. Given that small mammals may respond more naturally to artificial nests that closely simulate natural nests, exteriors of above-ground nests should be modified with natural plant materials to imitate nests of the bird species of interest. Appropriate choices of egg types for artificial nest studies require some advance knowledge of the

composition of the predator community. Composition of predator communities could be ascertained *a priori* by conducting point counts (Reynolds *et al.* 1980) to census avian predators and diurnal squirrels, and by live-trapping small nocturnal mammals, though the latter would be labor intensive. Alternatively, predator species composition could be assessed with various artificial nest experiments. First, hair catchers or cameras could be used in concert with finch eggs to identify predators with minimal interference from olfactory cues. Secondly, for each replicate plot of an experimental treatment, one-half of randomly deployed nests could contain plasticine eggs and one-half could contain finch eggs (avoiding nearest-neighbor effects would be imperative). Thirdly, a cross-over experimental design would permit comparisons of predation rates using finch and plasticine eggs among and within replicate plots. Relative to natural eggs, plasticine eggs could allow twice as many predators to be identified. Nonetheless, any method of predator identification has inherent biases (Yahner and Wright 1985, Angelstam 1986, Major 1991, Fenske-Crawford and Niemi 1997, Brown *et al.* 1998, Marini and Melo 1998).

Domestic finch eggs are likely the best alternative to wild songbird eggs for artificial nest studies because they capture predation events by all members of the predator community, and provide a more natural food source that could evoke natural behavior from predators. If small mammals (diurnal or nocturnal) dominate the predator community, then finch eggs rather than quail or plasticine eggs should be used to examine relative predation rates. Either quail or finch eggs could be used for predator communities dominated by large mammals or birds. In conclusion, implications of using artificial nests must be fully understood if these nests are to be used to test hypotheses under realistic conditions.

6. A COMPARISON OF DENSITY AND REPRODUCTIVE INDICES OF SONGBIRDS IN YOUNG AND OLD BOREAL FOREST

6.1 INTRODUCTION

Point counts and spot-mapping are popular methods to survey birds at landscape and local scales, respectively. As attention focuses on why some populations of migratory songbirds are declining (Robbins *et al.* 1989, Rappole and McDonald 1994, Sauer *et al.* 1995), complementary methods that incorporate measures of fitness become more important, particularly for rare or endangered species (Vickery *et al.* 1992a). Direct measurements of nesting success provide crucial information on productivity, recruitment, and life history (Martin 1992). Characteristics of occupied sites can then be related to productivity rather than bird presence or density, providing a stronger foundation for the development of conservation strategies (Pulliam 1988, Van Horne 1983).

Although invaluable information is obtained by measuring productivity compared to the other bird-census techniques, logistics often make nest-searching arduous and unproductive (Hobbs and Hanley 1990). Nest-searching is labor-intensive (Ricklefs and Bloom 1977, DeSante and Geupel 1987) and may require up to 40-50 ha plots (Martin and Geupel 1993, Ralph *et al.* 1993) to locate the minimum number of nests per species needed for an adequate estimate of nesting success (Hensler and Nichols 1981). Ground nests, typical of many neotropical migrant songbirds, as well as canopy nests are generally more difficult to find than shrub nests (Martin 1992, Ralph *et al.* 1993). Nests that are detected by investigators may not represent a random sample (Vickery *et al.* 1992a). Moreover, nest-searching and monitoring may disturb birds during a critical part of the breeding cycle, reducing reproductive success, which is especially detrimental for rare species (Vickery *et al.* 1992a).

Recently, studies have shown that frequencies of certain reproductive behaviors,

representing various portions of the breeding cycle, can reliably index songbird breeding productivity in grassland habitats (Vickery *et al.* 1992a, Hartley 1994, Dale *et al.* 1997). With growing conservation concerns for songbirds breeding in temperate and northern boreal forests (Schieck *et al.* 1995), it is important to assess the feasibility of detecting reproductive behaviors and fledglings in forested habitats and potentially using these measures of productivity as a surrogate of nest success. Observations of reproductive behaviors or fledged young could then be used in lieu of nest success to test critical assumptions that underpin management and conservation initiatives for songbirds.

Habitat quality may be defined as the capability of land to maintain and produce animals of a given species (i.e., carrying capacity); however, due to absence of these direct measures, habitat quality has become synonymous with measures of habitat use such as density, particularly in management applications (Hobbs and Hanley 1990). The latter is based on the assumption that more individuals of a species will occur in higher quality habitat. Furthermore, it is often assumed that density is associated positively with survival and reproduction of individuals (Van Horne 1983, 1986; Prosser and Brooks 1998). However, areas of high abundance may not necessarily be suitable habitat; they may represent "sinks" rather than "sources" (Pulliam 1988, Donovan *et al.* 1995, Dias 1996, Purcell and Verner 1998). High numbers of juvenile males or "floaters" in poor quality habitat (Van Horne 1983, Roberts and Norment 1999), site fidelity (Rotenberry and Wiens 1978), and annual variability in predation rates, abiotic factors, and food may inflate or deflate density estimates (Blake *et al.* 1994). Despite recent evidence that density is often not related to habitat quality (Van Horne 1983, Vickery *et al.* 1992b), existence of such a relationship seems tacitly accepted in the literature.

I compared songbird densities, indices of reproductive behavior, and detections of fledglings in young and old mixedwood boreal forest stands in west-central Alberta. These age-classes were chosen because they relate to current concerns regarding effects of short-rotation forestry practices on forest bird communities (Schieck *et al.* 1995). I also tested the hypothesis that density is related positively to nesting effort and success as measured by my index of reproductive behavior and detections of fledglings, to assess the efficacy of such census techniques to answer relevant ecological questions.

6.2 STUDY AREA AND METHODS

Spot-mapping grids were located in boreal mixedwood forest stands of two age-classes, 25-year-old (logged 1970 to 73) and 75 to 100-year-old (post-fire), approximately 25 km north of Marlboro, Alberta (53°31'N, 116°45'W) in the (Boreal) Lower Foothills Natural Region. Canopies of young and old stands were composed mainly of trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), fir (*Abies* spp.), and balsam poplar (*P. balsamifera*) comprised most of the remaining canopy in young stands. Subcanopies, only present in old stands, consisted of white spruce, balsam poplar, and trembling aspen, in decreasing importance. Willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), low-bush cranberry (*Viburnum edule*), *Ribes* (spp.), and wild rose (*Rosa* spp.) characterized understories of young stands. Understories of old stands contained the same species, but green alder was most abundant followed by willow and buffaloberry (*Shepherdia canadensis*).

6.2.1 Spot-mapping

I established 9 ha spot-mapping grids, 300 m x 300 m (subdivided into 25 m x 25 m quadrats), ≥ 20 m from the nearest edge of six young and six old mixedwood stands. Young and old stands were visited 1 June to 7 July 1995, totalling 166.0 and 166.4 hours, respectively. Territories were spot-mapped (International Bird Census Committee 1970) between 0500 and 0900 hours 7-8 times per stand to obtain bird densities. Because territories could not be delineated unambiguously using 7-8 visits, but I was confident about number of individuals per stand, I determined bird species densities by first multiplying number of singing males and other individuals that were spatially separated from singing males but provided evidence of breeding (see below) by two for each visit. If there were no singing males or reproductive behaviors by other individuals recorded near an active nest, active nests also were multiplied by 2, to include these unrecorded breeding pairs. I averaged values for visits for each stand, then divided by the respective area to obtain bird species density. Within each visit, the 12 stands were randomly assigned to one of four observers to minimize observer bias. With four observers, all 12 stands were visited once over a 3-day period to complete a

rotation. Two young and two old habitat types were visited daily.

6.2.2 Reproductive Behavior And Success

Spot-mapping grid lines in young and old mixedwood stands were walked six-nine times between 1 June and 28 July 1995 to coincide with territory establishment, nest building, incubation, brooding, and fledging periods. During walks, conducted from about 0900 to 1300 hours, reproductive behavior and fledged young were monitored with total sampling times of 149.5 hours in young mixedwood and 145.5 hours in old mixedwood stands. Point of entry into stands was randomized for each visit. All reproductive behaviors and active nests observed during spot-mapping also were recorded. For each visit, bird species, sex, age (adult or fledgling), activity, and nest location were recorded. When a bird was encountered, its activity at the initial point of contact was recorded (Morrison *et al.* 1992). Reproductive observations included presence of apparently mated pairs; courtship display; transportation of nest material, food, or fecal sacs; bird calls indicative of nesting or brood rearing; distraction displays; and, observations of nests, nestlings, and fledglings (Martin and Geupel 1993). These observations were pooled into four major categories: pair or nest construction; clutch; nestlings; and fledglings. Singing was not included as a reproductive behavior as some males may halt territorial song when mated and other males that do not mate may continue singing (Gibbs and Wenny 1993).

6.2.3 Statistical Analyses

Comparisons of individual species densities (square root transformed) were made between young and old stands using a one-way analysis of variance (Zar 1984). Analysis of Covariance (ANCOVA), controlling for avian species density, was used to evaluate differences in indices of reproductive behavior and total frequency of fledglings (recorded during behavioral censuses and spot-mapping combined) between young and old mixedwood stands. When bird density was not significant, it was eliminated from ANCOVA models. Because behaviors indicative of breeding effort and success may not be considered equal (e.g., a clutch or even a brood does not equal fledged young) behaviors were summed in a weighted index as follows: clutches were multiplied by

two, broods were multiplied by three, and fledglings were multiplied by four. Bird densities, indices of reproductive behavior, and fledgling numbers were square root transformed to improve normality. For each species, Spearman rank correlation was used to examine the relationship of indices of reproductive behavior, following weighting, and frequency of fledglings versus bird density using 12 forest stands. Tests for curvilinearity and absence of nonlinear patterns on scatter plots supported using linear correlations. Only species with at least 20 reproductive observations and a minimum of 10 fledglings per stand age-class were analyzed for density-productivity patterns. Power analyses were performed, using GPOWER (Faul and Erdfelder 1992), to estimate the number of spot-mapping grids to detect differences between forest age-classes given power of 0.8, alpha of 0.05, and hypothesized effect sizes of 0.2, 0.5, and 0.8 (Cohen 1988). SAS (1990) was used for all other analyses at a significance level of 0.05.

6.3 RESULTS

Density of only two of 12 bird species (17%) differed between the two stand-ages (Table 6.1). Hermit Thrushes had greater densities in young stands and Yellow-rumped Warblers had greater densities in old stands (see Appendix B for scientific names). White-throated Sparrows and Mourning Warblers had the highest and lowest species density, respectively, in young and old stands.

Young stands ($n = 6$) were censused 14-17 times, combining behavioral censuses and spot-mapping, yielding a mean census coverage of 28.3 minutes/ha per visit ($SE = 1.4$, $n = 74$). Likewise, old stands ($n = 6$) were censused 15-16 times, yielding a mean census coverage of 27.2 minutes/ha per visit ($SE = 1.3$, $n = 76$). The index of reproductive behavior was greater in young stands for Dark-eyed Juncos, Orange-crowned Warblers, and Warbling Vireos, and greater in old stands for White-throated Sparrows (Table 6.2). When frequency of fledglings observed was compared between the two stand age-classes, productivity was greater for White-throated Sparrows in old stands (Table 6.3). Given a power of 0.8, an alpha of 0.05, and differences in indices of reproductive behavior of 20%, 50%, and 80% (i.e., effect sizes), total number of spot-mapping grids

Table 6.1. Mean (\pm SE) bird species and nest guild densities (individuals/100 ha) for young ($n = 6$) and old ($n = 6$) boreal mixedwood forest stands in west-central Alberta (June to July 1995). P values from Analysis of Covariance (Type III SS) are shown for stand-age.

Species/Guild ^a	Young	n^b	Old	n	P Stand-age ^c
Chipping Sparrow (A)	29 (13)	121	48 (11)	201	0.20
Dark-eyed Junco (G)	54 (9)	222	41 (5)	173	0.26
Lincoln's Sparrow (G)	34 (11)	149	9 (6)	40	0.06
White-throated Sparrow (G)	83 (20)	359	158 (31)	666	0.09
American Robin (A)	19 (5)	77	26 (8)	109	0.73
Hermit Thrush (G)	40 (12)	162	9 (3)	38	0.02
Swainson's Thrush (A)	36 (9)	153	61 (14)	253	0.29
Warbling Vireo (A)	55 (9)	229	75 (12)	313	0.16
Mourning Warbler (G)	4 (3)	18	8 (5)	33	0.71
Orange-crowned Warbler (G)	62 (9)	262	35 (14)	149	0.12
Tennessee Warbler (G)	54 (7)	227	37 (14)	158	0.14
Yellow-rumped Warbler (A)	77 (12)	315	131 (11)	547	0.01
Above-ground nesters	43 (5)	895	68 (7)	1423	0.004
Ground nesters	47 (5)	1399	42 (7)	1257	0.50

^a Letters in parentheses indicate membership in nest guilds (A = above-ground nesters; G = ground nesters).

^b n = total number of individual birds observed over seven or eight visits to each of six spot-mapping grids per stand-age.

^c P values are reported for $F_{1,11}$.

Table 6.2. Mean (\pm SE) index of reproductive behavior recorded for bird species and nest guilds in young ($n = 6$) and old ($n = 6$) boreal mixedwood forest stands in west-central Alberta (June to July 1995). P values from Analysis of Variance or Analysis of Covariance (Type III SS) are shown for overall model, stand-age, and covariate of bird density (individuals/ha).

Species/Guild ^b	Index of reproductive behaviors ^a		P Model ^c	P Stand age ^d	P Bird density ^d
	Young	Old			
Chipping Sparrow (A)	17.5 (5.7)	8.5 (3.8)	0.20	0.20	
Dark-eyed Junco (G)	73.8 (15.2)	28.2 (6.9)	0.03	0.03	
Lincoln's Sparrow (G)	13.2 (9.1)	4.5 (3.2)	0.05	0.52	0.02
White-throated Sparrow (G)	32.5 (8.5)	119.5 (22.5)	0.004	0.004	
American Robin (A)	10.5 (3.5)	12.2 (8.8)	0.04	0.13	0.02
Hermit Thrush (G)	14.0 (5.4)	4.5 (3.8)	0.14	0.14	
Swainson's Thrush (A)	4.7 (2.3)	12.5 (4.0)	0.29	0.29	
Warbling Vireo (A)	4.8 (1.9)	1.38 (1.3)	0.006	0.005	0.006
Mourning Warbler (G)	4.3 (3.9)	2.8 (1.8)	0.006	0.48	0.002
Orange-crowned Warbler (G)	23.8 (8.3)	1.5 (0.7)	0.003	0.003	
Tennessee Warbler (G)	18.8 (7.7)	8.3 (6.6)	0.004	0.30	0.003
Yellow-rumped Warbler (A)	66.3 (15.3)	57.7 (15.3)	0.78	0.78	
Above-ground nesters	20.8 (4.5)	18.4 (3.8)	0.70	0.70	
Ground nesters	25.8 (3.2)	24.2 (2.9)	0.72	0.72	

^a Behaviors associated with a clutch, brood, or fledglings were multiplied by two, three, and four, respectively, to weight behaviors based on importance.

^b Letters in parentheses indicate membership in nest guilds (A = above-ground nesters; G = ground nesters).

^c P values are reported for $F_{2,11}$.

^d P values are reported for $F_{1,11}$.

Table 6.3. Mean (\pm SE) frequency of fledglings recorded for bird species and nest guilds in young ($n = 6$) and old ($n = 6$) boreal mixedwood forest stands in west-central Alberta (June to July 1995). P values from Analysis of Variance or Analysis of Covariance (Type III SS) are shown for overall model, stand-age, and covariate of bird density (individuals/ha).

Species/Guild ^a	Frequency of fledglings		P Model ^b	P Stand age ^c	P Bird density ^c
	Young	Old			
Chipping Sparrow (A)	2.0 (0.8)	1.0 (0.6)	0.34	0.34	
Dark-eyed Junco (G)	10.2 (2.4)	4.5 (1.9)	0.09	0.09	
Lincoln's Sparrow (G)	1.7 (1.3)	0.8 (0.5)	0.06	0.29	0.02
White-throated Sparrow (G)	5.0 (1.4)	18.8 (4.1)	0.007	0.007	
American Robin (A)	1.3 (0.3)	2.3 (1.6)	0.05	0.34	0.01
Hermit Thrush (G)	1.7 (0.8)	1.0 (0.8)	0.52	0.52	
Tennessee Warbler (G)	2.7 (1.3)	0.8 (0.8)	0.26	0.26	
Yellow-rumped Warbler (A)	14.7 (3.5)	11.8 (3.9)	0.64	0.64	
Above-ground nesters	6.0 (1.4)	5.1 (1.3)	0.64	0.64	
Ground nesters	4.2 (0.7)	5.2 (0.7)	0.35	0.35	

^a Letters in parentheses indicate membership in nest guilds (A = above-ground nesters; G = ground nesters).

^b P values are reported for $F_{2,11}$.

^c P values are reported for $F_{1,11}$.

required to detect reproductive differences was 780, 126, and 45, respectively.

Positive correlations between bird species densities and indices of reproductive behavior or total frequency of fledglings observed were evident for 45% and 40% of species, respectively (Table 6.4). Lincoln's Sparrows, White-throated Sparrows, American Robins, and Tennessee Warblers were the only species to show this trend for frequency of reproductive behaviors and fledglings.

6.4 DISCUSSION

6.4.1 Density and Reproductive Indices

Few differences were detected in individual species densities between forest age-classes, which may be related to the small age difference (50-75 years) between treatments and high variance among replicates. Other factors, such as annual variation or sampling error, also may have also contributed to a poor distinction in bird density between stand-ages. Additionally, some species may cue on microsite characteristics common to both seral stages rather than vegetation patterns unique to each successional stage. On the other hand, above-ground nesting species were more common in older stands (Table 6.1), perhaps reflecting greater vegetation diversity on these sites (Westworth and Telfer 1993, Schieck *et al.* 1995).

The index of reproductive behavior was greater in young than old stands for three species (Table 6.2), whereas the index for White-throated Sparrows was almost four times greater in old than young stands. Likewise, fledgling White-throated Sparrows were detected more frequently on older stands (Table 6.3). Several factors contributed to my inability to discriminate between stand-age groups. Forest birds most amenable to use of reproductive indices or detections of fledglings were abundant, ground-nesting species. Being abundant enhanced the probability of detecting behaviors associated with breeding productivity, whereas ground-nesting species and their fledglings were generally more conspicuous than above-ground nesting species. Moreover, only one of four species that differed in the index of reproductive behavior between young and old stands differed in the frequency of fledged young. This suggests that all indices of

Table 6.4. Spearman rank correlation of bird species density (individuals/ha) with index of reproductive behavior and frequency of fledglings observed in young ($n = 6$) and old ($n = 6$) boreal mixedwood stands in west-central Alberta (June to July 1995).

Species (individuals/ha)	Index of reproductive behavior ^a		Frequency of fledglings	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Chipping Sparrow	-0.13	0.68	-0.10	0.76
Dark-eyed Junco	0.63	0.03	0.36	0.24
Lincoln's Sparrow	0.67	0.02	0.57	0.05
White-throated Sparrow	0.62	0.03	0.60	0.03
American Robin	0.61	0.03	0.61	0.03
Hermit Thrush	0.67	0.02	0.43	0.16
Swainson's Thrush	0.53	0.08	0.30	0.34
Warbling Vireo ^b	0.36	0.25		
Orange-crowned Warbler	0.38	0.22	0.47	0.12
Tennessee Warbler	0.85	0.001	0.58	0.05
Yellow-rumped Warbler	-0.23	0.47	-0.32	0.31

^a Behaviors associated with clutches, broods, or fledglings were multiplied by two, three, and four, respectively, to weight behaviors based on importance.

^b Minimum number of fledglings required for statistical analysis was not attained.

breeding effort and success are not equal and supports the need to weight behaviors accordingly (Vickery *et al.* 1992a). Other indices of body condition (e.g., body mass, blood cell counts), population demographics (e.g., age ratio), or territory size (Hunt 1996) that reflect population health better and are likely easier to obtain than density also may provide alternatives to indices of reproductive behavior (Schamberger and O'Neil 1986).

The minimum index of reproductive behavior and number of fledglings I selected as a cut-off to conduct statistical analyses were attained for only 36% of migratory songbird species present in young and old stands. Moreover, differences between forest age-classes in the index of reproductive behavior and number of fledglings were detected for only 25% and 13% of the remaining species, respectively. White-throated Sparrows were the only species to show a tentative trend with high densities, indices of reproductive behavior, and detections of fledglings in old stands. The remaining five species that demonstrated significant differences between stand-ages for either density or the index of reproductive behavior did not show consistent trends for the three response variables of density, reproductive indices, and fledgling numbers. With similar densities in young and old mixedwood stands and low statistical power to detect density differences, it was difficult to evaluate adequately the assumption that reproductive success was positively correlated with density. If higher indices of reproductive behavior of species in young versus old stands were real, even though bird densities did not differ, it suggests that density and habitat quality were not correlated positively, corroborating other studies (Maurer 1986, Vickery *et al.* 1992b, Purcell and Verner 1998, Roberts and Norment 1999). Correlations between bird density and either measure of productivity was weak for one-half of all species and density-reproductive success patterns among guild members also were inconsistent.

Not only were relationships between my measures of productivity and density inconsistent, but results also contrasted other studies of habitat use. Warbling Vireos and Dark-eyed Juncos had similar densities across forest age-classes, yet these birds are typically associated with stands older than 25 years (Westworth *et al.* 1984, Kirk *et al.* 1996). Furthermore, Juncos often use logged areas, similar to my young stands, more

than unlogged areas, whereas Warbling Vireos are less discriminatory across disturbance and nondisturbance regimes (Kilgore 1971, Franzreb 1983, Hagar 1999). Indices of reproductive behavior for Orange-crowned Warblers and White-throated Sparrows, however, appeared consistent with the young and old successional stages they typically inhabit, respectively (Schieck *et al.* 1995, Kirk *et al.* 1996). Inconsistencies in patterns of productivity and habitat associations, particularly for species like Warbling Vireos and Yellow-rumped Warblers that tend to nest and forage in canopies (Franzreb 1983, Westworth *et al.* 1984), may be related to methodological problems associated with censusing reproductive behaviors and fledglings. A visibility bias probably existed in my study because observers were more likely to detect reproductive behaviors or fledged young in young than old stands due to their lower canopy height. To help account for the confounding effect of bird species detectability, it may be helpful to incorporate a correction factor into the analysis based on foliage height and density for canopy species (Schieck 1997).

Sampling effort was comparable to Vickery *et al.*'s (1992a) study: thus, the primary drawbacks of my study were the number of replicate spot-mapping grids required to obtain optimal power and the inability to verify reproductive indices and fledgling estimates using active nests. My forested stands were visited 14-17 times with a census coverage of 28 minutes/ha per visit (9 ha grids), versus 10-17 visits with a census coverage of 5 minutes/ha per visit (15 ha grids) used previously for grassland plots (Vickery *et al.* 1992a). My sampling effort, in only one year, for songbird reproductive behaviors and fledglings per stand-age in boreal mixedwood forest (old = 311 hours; young = 316 hours) was about 75% of that in grasslands over three years (~421 hours; Vickery *et al.* 1992a). Observed trends in reproductive effort and success might be more fully supported if sample sizes and, subsequently, statistical power were increased. However, power analyses indicated sample sizes larger than may be logistically possible were required to obtain acceptable power. Moreover, logistical difficulties in locating nests prevented me from comparing indices of reproductive behavior or fledgling numbers with nesting success for each species. Thus, in forested habitats, the use of behavioral indices or detections of fledglings appears too labor-intensive, requiring a

large number of independent spatial replicates to be sampled over multiple years. Vickery *et al.* (1992a), Hartley (1994), and Dale *et al.* (1997) successfully used reproductive behavior to index nest success, but they conducted studies in grasslands where bird visibility was less restricted and nests were easy to detect relative to forested habitats.

6.4.2 Conclusions

Using indices of reproductive behavior and observations of fledged young to estimate reproductive success of songbirds in mixedwood forests appears impractical because visual contact with songbirds by investigators is difficult in structurally complex habitats. Indices of reproductive behavior for some species may be as high or higher in young versus old forest seral stages on a per capita basis, yet caution is advised in developing management decisions regarding forest rotation age until further studies are conducted to corroborate my findings. Correlations of indices of reproductive behavior and fledgling numbers versus density for bird species were inconsistent concerning significance and direction, indicating that density and habitat quality were not tightly linked. Because differences in reproductive activity between stand-ages and positive correlations between density and reproductive activity likely do exist, additional statistical power may be helpful (Johnson 1999). However, numbers of spot-mapping grids requiring censusing for reproductive behaviors or fledged young to achieve a power of 80% may be substantial.

7. SYNTHESIS

Avian populations and communities are influenced by multiple biotic and abiotic factors. Predators, competitors, parasites, climate, resource quality and quantity and stochasticity are among the central forces that determine population change and community structure. Major challenges for ecologists are to measure the relative strengths of these forces, understand their interactions, and so explain observed patterns of bird distribution and abundance. The general goal of this study was to determine if predation was an important process structuring forest bird communities, in addition to habitat structure and floristics, and also to test the reliability of methodologies that are currently used widely to evaluate reproductive success in songbirds.

7.1 PREDATORS AND SONGBIRD COMMUNITY STRUCTURE

Although predation is the primary cause of nesting mortality (Martin 1992), until recently, community ecology has neglected predation as a process structuring avian communities (Martin 1988a, 1993a). It has been hypothesized that selective predation on similar nests of coexisting species diversify bird communities. Results from my research using natural songbird communities suggest that higher predator diversity and/or abundance increases songbird diversity (Chapter 2). Detection of this pattern in two geographical locations does not provide unequivocal corroboration of the predation hypothesis, particularly when predation did not seem to be a strong selective force in partitioning nest-space based on results from artificial nests in one of the two study areas (Chapter 3). Disagreement between results of these two chapters may be explained by deficiencies associated with artificial nests. Hence, identifying predators as an alternative selective pressure driving avian communities is only a first step and must be followed by true tests of its effects on pattern by isolating processes. Also, measuring the relative strengths and teasing apart synergistic effects of several contributing

mechanisms requires further investigation; such tests will be more complete than attempts to attribute avian community patterns to single factors (Brown 1988, Tellería *et al.* 1992, Martin 1988a). Although predation seemed to be a credible explanation for observed patterns of species diversity, it is unlikely that a single process was operating consistently over such a broad array of species. Rather, several mechanisms such as predation and food resources were acting, potentially in concert, to diversify bird communities via increased nesting and foraging niches, respectively (Wiens 1989b, Lawton 1996). It is also possible that positive associations between predator and bird diversity were spurious with predators and prey responding similarly to unmeasured factors such as vegetation, food abundance, and environmental variation.

How susceptible coexisting species with similar nest types are to predation is probably closely linked to the composition of the predator community in boreal forest (Chapter 4, Rangen *et al.* 1999). Predators such as red squirrels (*Tamiasciurus hudsonicus*) and jays that rely on visual cues and can easily depredate nests on the forest floor or in tall trees may more strongly influence partitioning of nesting microhabitat than mice that rely on olfaction for food detection and forage on the ground. Visually-oriented predators may be more likely to develop search images related to nest appearance and nest height more than mice. Though red squirrels and mice are considered common predators of songbird nests, their roles in structuring avian communities are uncertain. The role of mice is particularly unclear because mice were rarely documented as nest predators until plasticine eggs were used in artificial nest experiments (Bayne *et al.* 1997). At natural nests, however, parent birds are present and natural eggs are harder to penetrate than plasticine eggs; plasticine odors attract mice (Chapter 5, Rangen *et al.* 2000a). Squirrels and mice may also exert opposing forces of selection on nest-site choice and nest partitioning because they tend to depredate different nest guilds; thus, experiments that manipulate predator species will provide more robust tests of predator effects.

Detecting patterns of songbird diversity that are induced by predators in boreal forest is complicated by extensive variability in predator communities and habitat. Experiments that manipulate natural populations are therefore needed to control

confounding factors and to provide less ambiguous evidence of predation processes (Wiens 1989b). Experimental manipulations of the predator community (e.g., additions, removals) are alternative approaches that create variation in the abundance of one or more predator species. Red squirrels and small mammals (i.e., mice/ voles) have several characteristics that facilitate manipulation: 1) they are considered primary predators of ground- and above-ground nesting songbirds in boreal forest; 2) they are predators of songbirds and not competitors; and, 3) they have been used extensively in manipulative experiments in forested habitats (Klenner 1991, Larsen and Boutin 1995). Therefore, long-term studies of this nature would be extremely valuable.

7.2 DEVELOPMENT OF FIELD METHODS FOR DETECTION OF PATTERNS

To detect population and community patterns that are not artifacts of investigative techniques, methods used to derive estimates of avian reproductive success must be assessed critically. Part of my research focused on validating two methodologies associated with songbird productivity. First, indirect measurements of nesting success, such as reproductive indices, provide crucial information on productivity, recruitment and life history (Chapter 6, Rangen *et al.* 2000b). Thus, I assessed the feasibility of detecting reproductive behavior of songbirds and the occurrence of fledglings in forested habitats, and of using these measures of productivity as a surrogate for nesting success.

Drawbacks associated with detecting reproductive behavior in forests and using related data to address ecological and management-related hypotheses were highlighted. For example, I found that behaviors of ground nesters were easier to detect than that of above-ground nesters, and visibility of birds may be impaired in high, dense canopies. These data also strongly suggest that songbird management decisions should not be based on an assumed positive correlation of density and reproductive success (Van Horne 1983, Pulliam 1988), due to inconsistencies in direction and magnitude of these relationships.

Second, artificial nests are commonly used as a tool to assess nest success across habitat types (Chapter 5, Rangen *et al.* 2000a). Nonetheless, the reliability of experimental nests and dummy eggs to document rates of predation is not well known.

This research is significant because it shows that simple modifications of wicker nests may not be adequate to simulate natural nests: however, choice of egg type appears critical in obtaining more natural patterns of predation. Researchers claim that mice are key predators of songbird eggs based on artificial-nest studies that use plasticine eggs (Bayne *et al.* 1997, Hannon and Cotterill 1998). This may not be true: my work showed that plasticine eggs attract small mammals and are more easily penetrated than natural eggs. This research should lead future investigations to determine which groups of nocturnal mammals comprise a large portion of the predator community before choosing the most appropriate type of artificial nest or dummy egg. Using artificial nest and egg types that match the predator community will yield more realistic tests that increase our understanding of songbird habitat and songbird-predator relations.

7.3 MANAGEMENT IMPLICATIONS

The nature and intensity of nest predation, and whether predators are a driving force in the diversification of nesting niches and songbird communities, have implications for sustainable forestry. Forest managers have focused primarily on the importance of vegetation structure and composition in maintaining viable populations of songbirds and maximizing avian diversity at the stand and landscape level (Bonar *et al.* 1990). To more fully investigate mechanisms influencing the structure of avian communities, large manipulative experiments, which incorporate current logging or silvicultural practices, can create variation in vegetation, predator communities, and other factors needed to test adequately competing hypotheses. If, in fact, predation pressure on songbird nests differs among predator species, then knowledge of how logging and silvicultural practices (e.g., short-rotation logging, removal of competing vegetation, monocultures, stand juxtaposition) affect specific predators will subsequently provide information on potential predator-prey interactions and avian community structure and reproductive success. To effectively mitigate predator effects on songbird communities, predator species that develop search images, have density-dependent predation, and potentially contribute to nest-niche diversification must be identified. For example, if squirrels and corvids provide stronger selection pressure to diversify songbird communities than

mice, then management prescriptions for predators as they relate to songbird diversity will differ for individual species.

When predator-mediated patterns of songbird community structure, habitat occupancy, and reproductive success are elucidated, predator-prey interactions can be linked with vegetation and competition in community habitat suitability index (HSI) models. These models are management tools used to facilitate forest and wildlife inventories, impact-assessment, mitigation, and the design of wildlife management goals (Schamberger and O'Neil 1986, Van Horne and Wiens 1991, Schroeder and Haire 1993). By including effects of predators and intra- and inter-specific competition in HSI models, the predictability of avian-habitat relationships should be enhanced leading to land management practices that better address conservation issues and undertake remedial and preventative measures. Furthermore, intensive investigations of processes influencing survival and productivity can be linked with extensive studies that evaluate density-habitat correlations to improve the reliability of HSI models.

Forest ecologists have expressed concern about negative effects of forest fragmentation on songbird communities (Paton 1994, Schmiegelow *et al.* 1997). Extensive work with artificial nests containing quail eggs tends to show that predation rates are higher in fragmented versus contiguous forest (Wilcove 1985, Small and Hunter 1988, Burger *et al.* 1994). Haskell (1995b) reexamined current dogma about predation in forest fragments and found high rates of predation in large patch sizes when predators were small mammals and plasticine eggs were used. Because my work indicated that small mammals rarely break quail eggs, previous interpretations of high predation in fragmented forest may be due to poor documentation of predation events by small mammals that use forest interior (Wauters *et al.* 1994, Mills 1995, Sekgororane and Dilworth 1995). High nest predation rates in forest interior, however, may be confounded by attracting small mammals to plasticine eggs in artificial nests. Thus, further research is required before management strategies are adopted that consider forest edges to be "ecological traps" for songbirds (Gates and Gysel 1978, Paton 1994). Overall, an understanding of predator-prey relations and reliable methods used to obtain

such patterns, are critical if managers are to implement conservation initiatives for songbirds.

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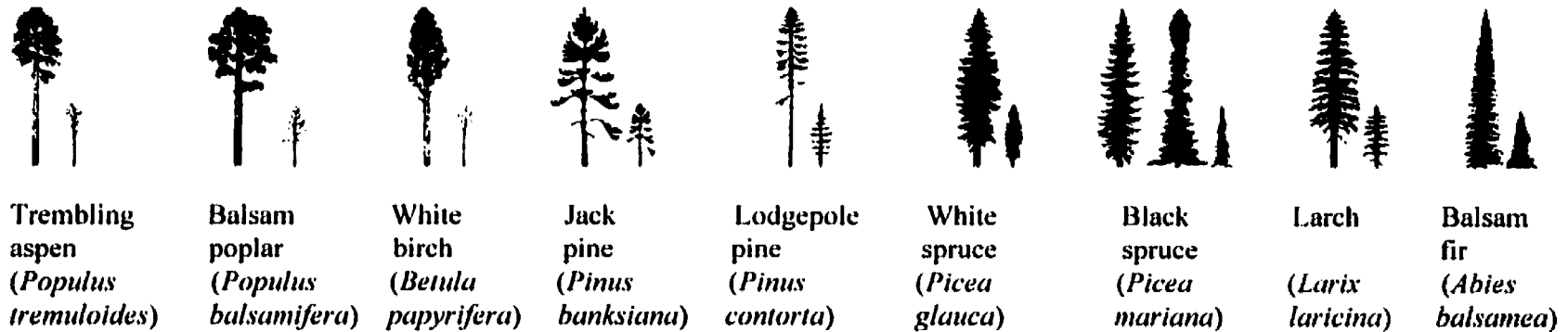
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APPENDIX A. DIAGRAMS OF REPRESENTATIVE FOREST STAND TYPES USED IN CHAPTERS 2-6.

Site diagrams provide a visual representation of tree species composition and stand structure within sites used to conducted field studies in Chapters 2-6. The objective was to provide qualitative rather than quantitative information. Relative frequencies of tree species, tree heights, shrub densities and heights, and snag densities and heights were used to develop Figures A.1. - A.29. When snag data were unavailable, other sources of information were used to estimate snag numbers (i.e., Beckingham *et al.* 1996a, Beckingham *et al.* 1996b, Sulistiyowati 1998). Diagrams were constructed similar to those used to classify ecosites in Alberta and Saskatchewan to allow cross-referencing for additional site information not obtained in this study (Beckingham *et al.* 1996a, Beckingham *et al.* 1996b).

Legend for tree species used in Figures A.1. - A.29.



Legend for shrubs used in Figures A.1. - A.29.

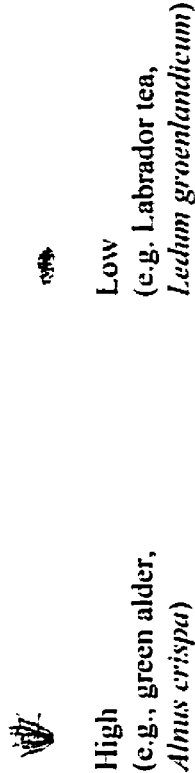


Figure A.1. Young deciduous stands in west-central Alberta.

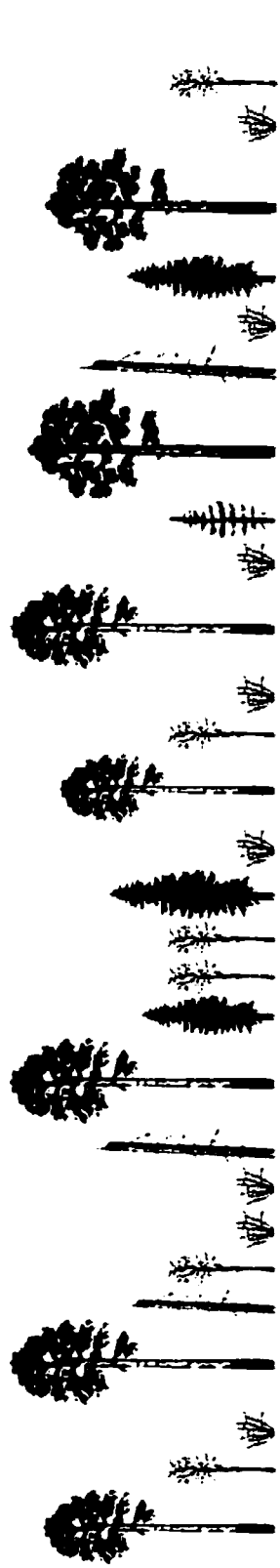


Figure A.2. Mature deciduous stands in west-central Alberta.

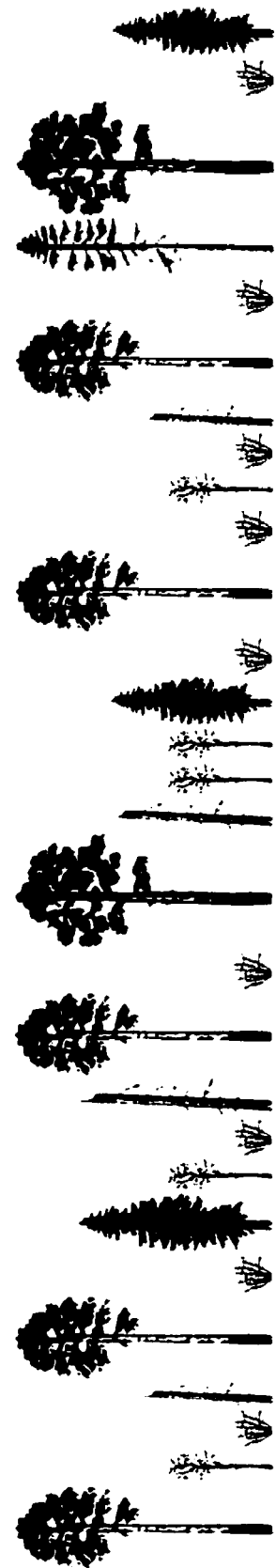


Figure A.3. Old deciduous stands in west-central Alberta.

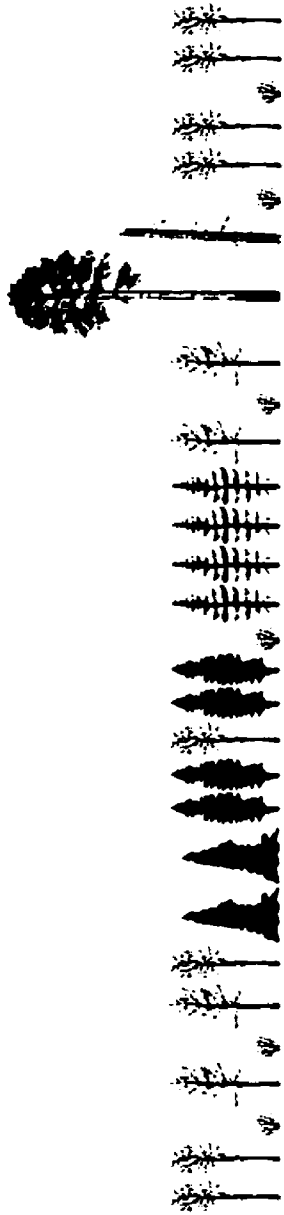


Figure A.4. Young mixedwood stands in west-central Alberta.

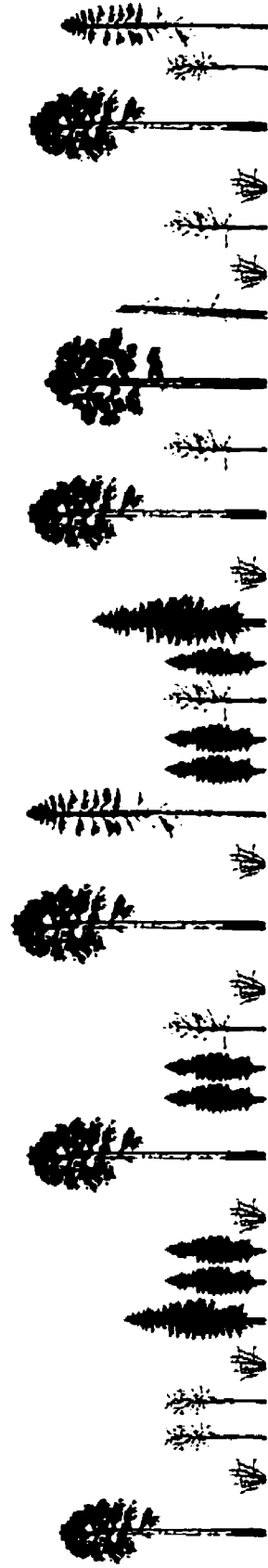


Figure A.5. Mature mixedwood stands in west-central Alberta.

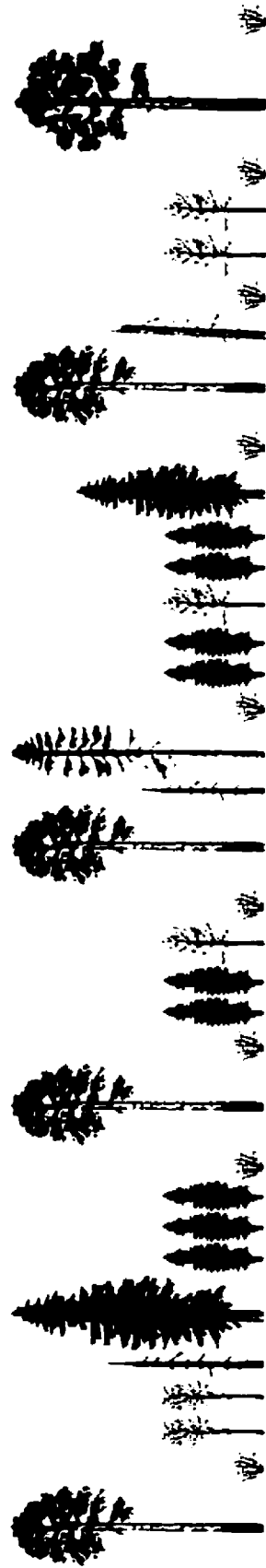


Figure A.6. Old mixedwood stands in west-central Alberta.

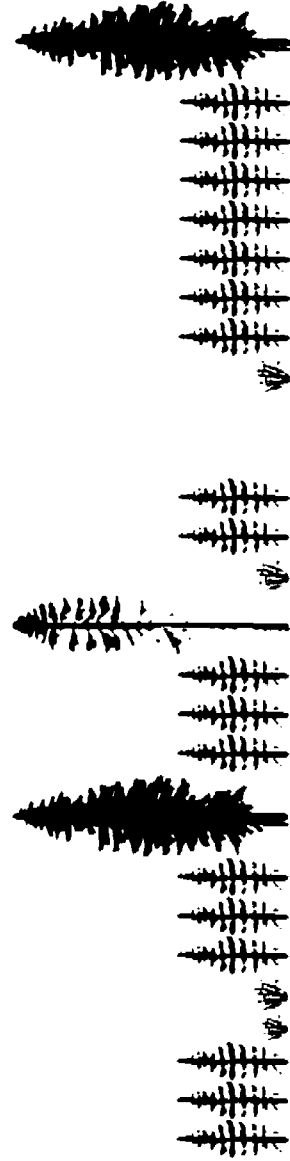


Figure A.7. Young lodgepole pine stands in west-central Alberta.

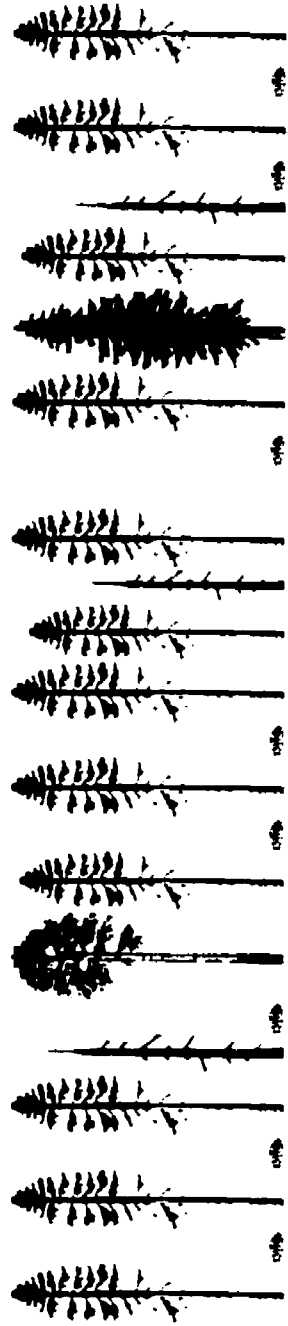


Figure A.8. Old lodgepole pine stands in west-central Alberta.



Figure A.9. Mature black spruce stands in west-central Alberta.

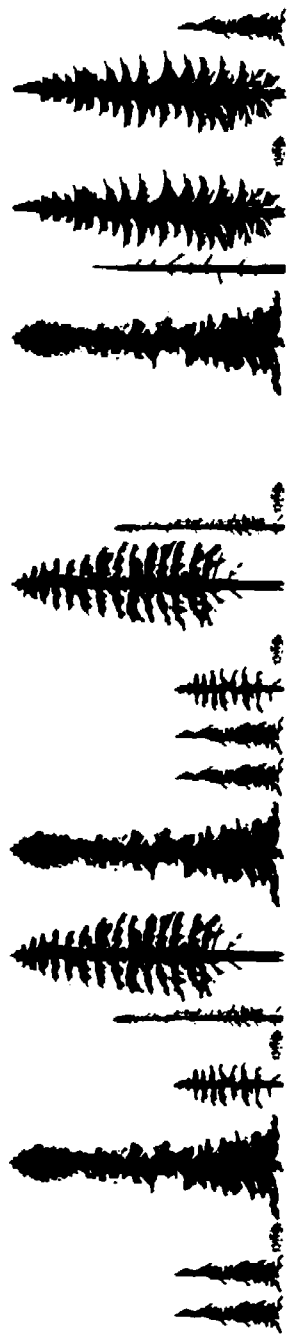


Figure A.10. Old black spruce stands in west-central Alberta.



Figure A.11. Old white spruce stands in west-central Alberta.



Figure A.12. Young spruce-fir stands in west-central Alberta.



Figure A.13. Mature spruce-fir stands in west-central Alberta.

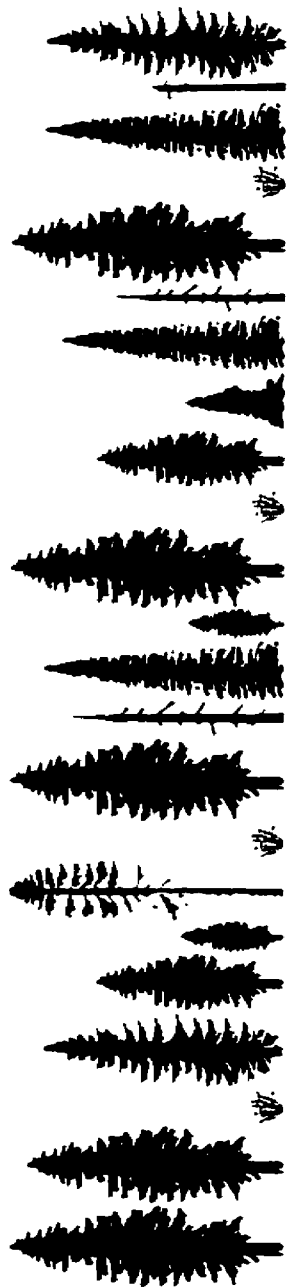


Figure A.14. Old spruce-fir stands in west-central Alberta.

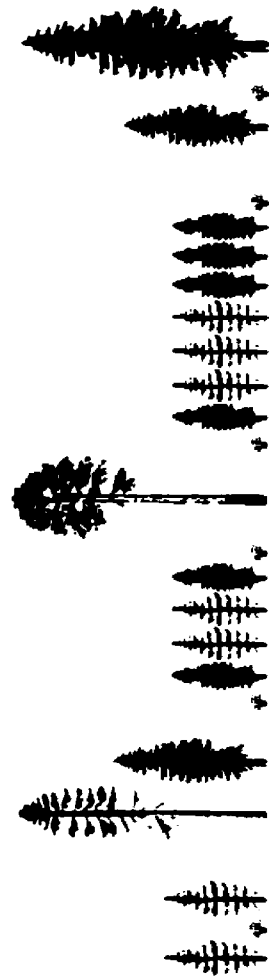


Figure A.15. Young spruce-pine stands in west-central Alberta.

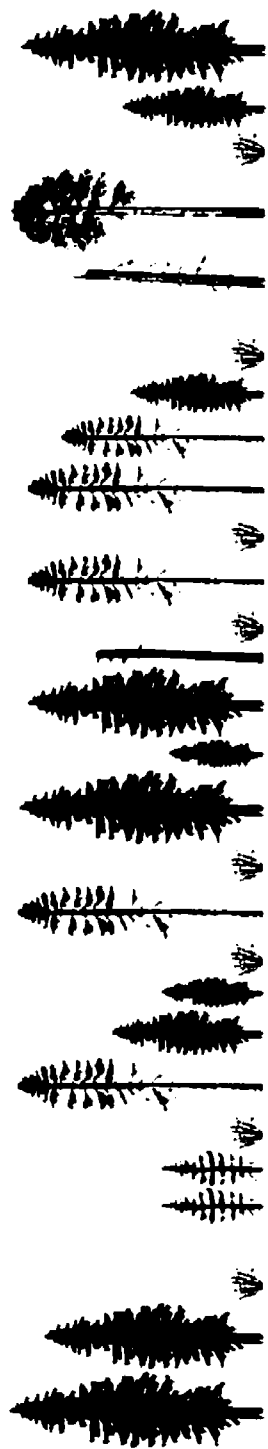


Figure A.16. Mature spruce-pine stands in west-central Alberta.



Figure A.17. Old spruce-pine stands in west-central Alberta.

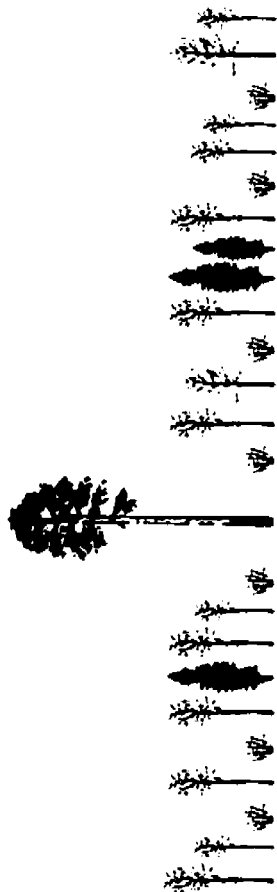


Figure A.18. Young aspen stands in central Saskatchewan.

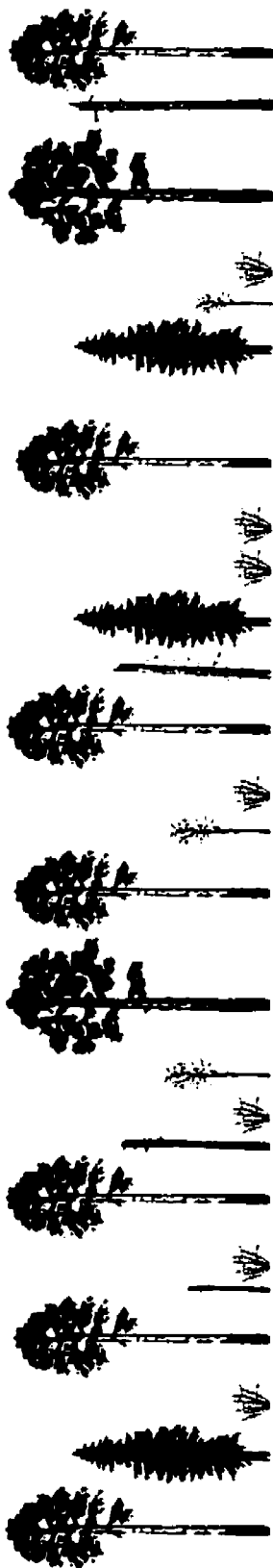


Figure A.19. Old aspen stands in central Saskatchewan.

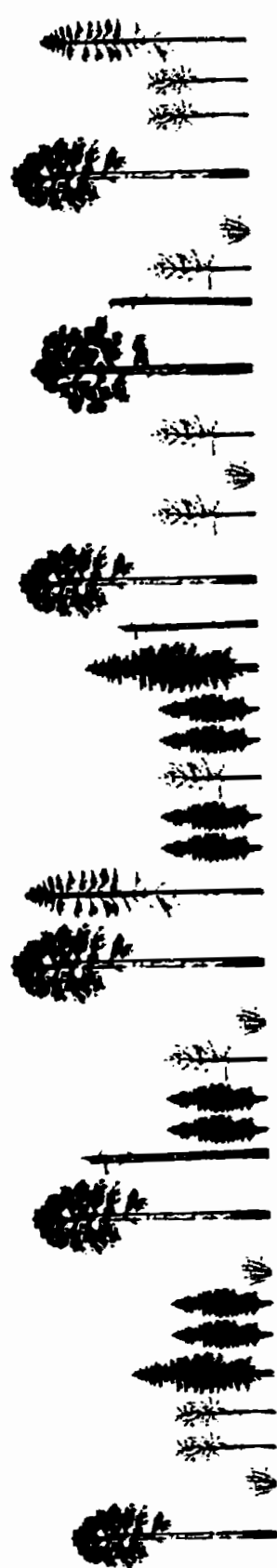


Figure A.20. Mature mixedwood stands in central Saskatchewan.

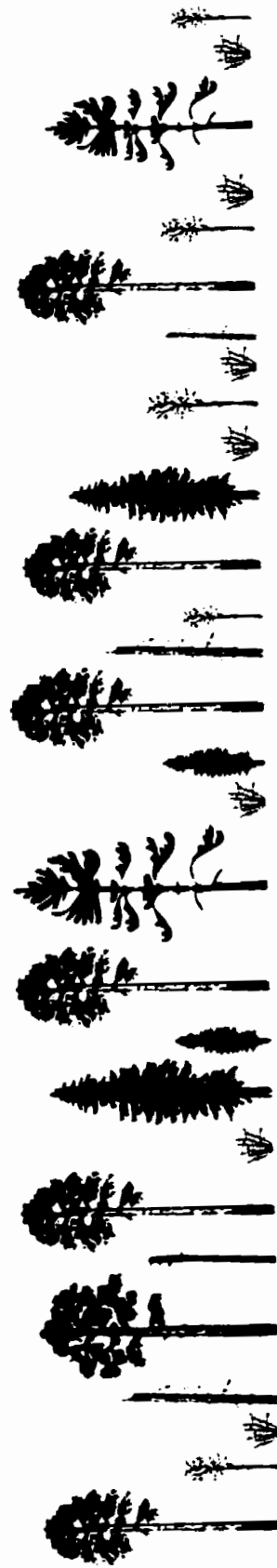


Figure A.21. Old mixedwood stands in central Saskatchewan.



Figure A.22. Young jack pine stands in central Saskatchewan.



Figure A.23. Mature jack pine stands in central Saskatchewan.



Figure A.24. Old jack pine stands in central Saskatchewan.

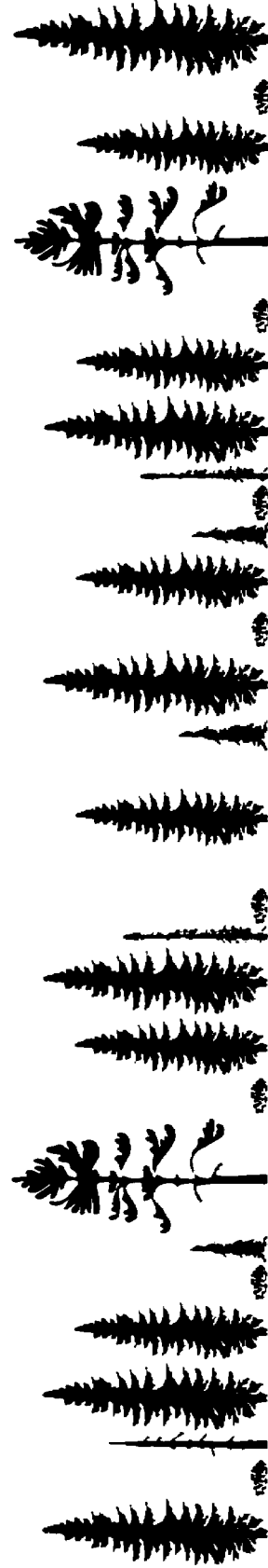


Figure A.25. Old black spruce stands in central Saskatchewan.

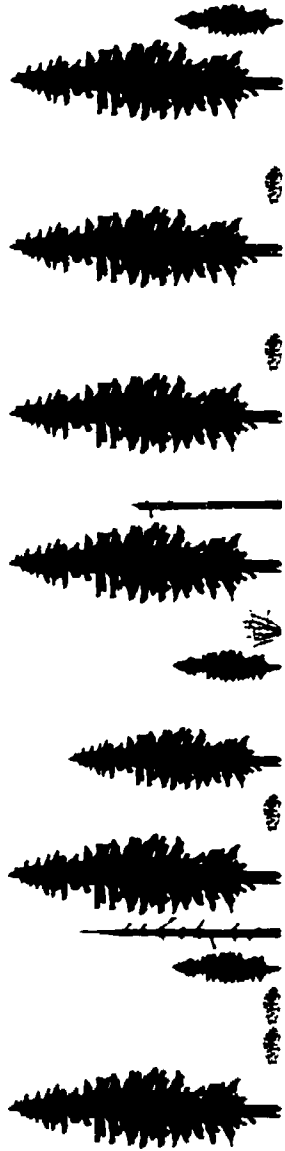


Figure A.26. Old white spruce stands in central Saskatchewan.

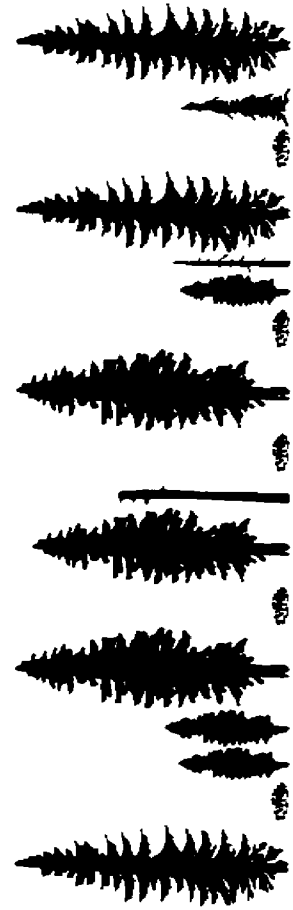


Figure A.27. Old black spruce-white spruce stands in central Saskatchewan.

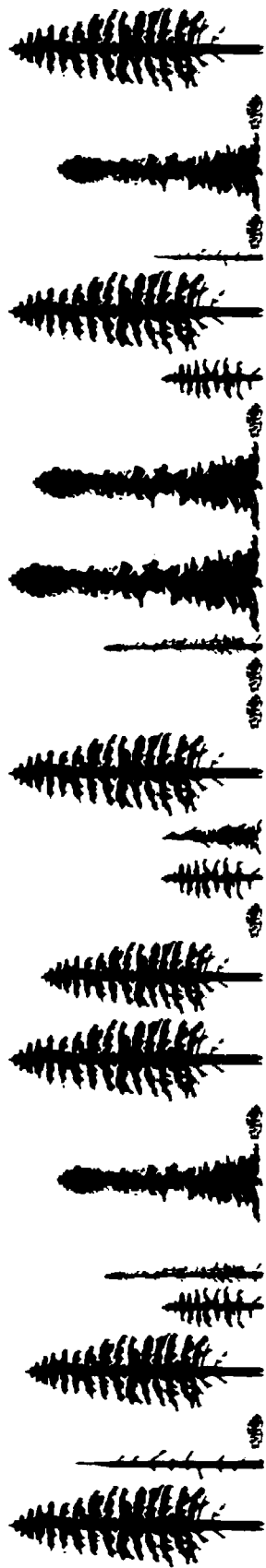


Figure A.28. Old larch stands in central Saskatchewan.

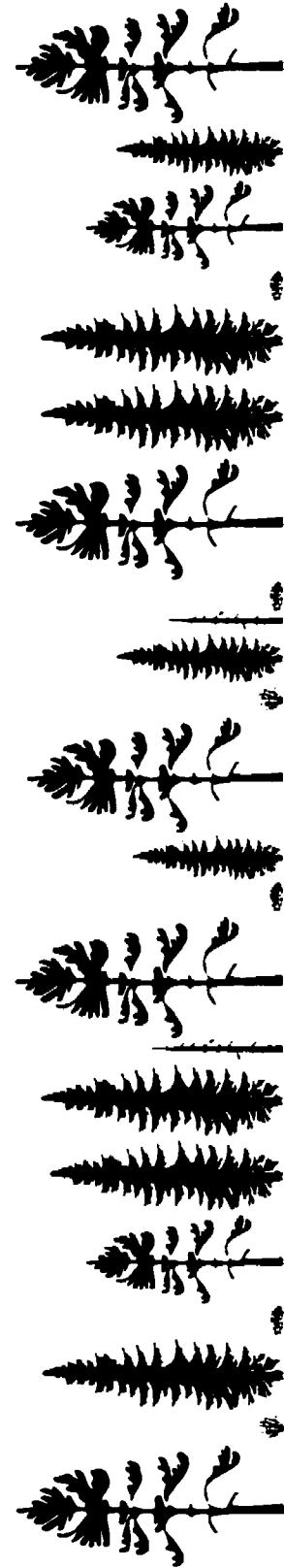


Figure A.29. Old jack pine-black spruce stands in central Saskatchewan.

APPENDIX B: BIRD SPECIES ON STUDY AREAS

Table B.1. Common names, American Ornithologists' Union (AOU) codes, scientific names, nest locations, and foraging guilds of bird species comprising communities in the Foothills Natural Region of Alberta and Mid-boreal and Churchill River Upland Ecoregions of Saskatchewan.

Common name	AOU code	Scientific name	Nest location ^a	Foraging guild ^b
Alcedinidae				
Belted Kingfisher*	BEKI	<i>Ceryle alcyon</i>	A	HD
Bombycillidae				
Bohemian Waxwing	BOWX	<i>Bombycilla garrulus</i>		FG
Cedar Waxwing	CEWX	<i>Bombycilla cedorum</i>	S,CT,DT	FG
Certhiidae				
Brown Creeper	BRCR	<i>Certhis americana</i>	A	BG
Charadriidae				
Killdeer	KILL	<i>Charadrius vociferus</i>	G	GG
Columbidae				
Mourning Dove*	MODO	<i>Zenaida macroura</i>	G,CT,DT	GG
Emberizidae				
Bay-breasted Warbler*	BBWA	<i>Dendroica castanea</i>	CT	FG
Black and White Warbler*	BWWA	<i>Mniotilta varia</i>	G	BG
Blackburnian Warbler	BLWA	<i>Dendroica fusca</i>	CT	FG
Black-throated Green Warbler*	BTGW	<i>Dendroica virens</i>	CT	FG
Canada Warbler*	CAWA	<i>Wilsonia canadensis</i>	G	FG
Cape May Warbler*	CMWA	<i>Dendroica tigrina</i>	CT	FG
Chestnut-sided Warbler*	CSWA	<i>Dendroica pensylvanica</i>	S	FG
Common Yellowthroat †	COYE	<i>Geothlypis trichas</i>	S	FG
Connecticut Warbler	COWA	<i>Oporornis agilis</i>	G	GG
MacGuillivray's Warbler †	MGWA	<i>Porornis tolmiei</i>	CT	FG
Magnolia Warbler	MAWA	<i>Dendroica magnolia</i>	CT	FG
Mourning Warbler	MOWA	<i>Oporornis philadelphia</i>	G	FG
Nashville Warbler*	NAWA	<i>Vermivora ruficapilla</i>	G	FG
Northern Waterthrush	NOWA	<i>Seiurus noveboracensis</i>	G	GG
Orange-crowned Warbler	OCWA	<i>Vermivora celata</i>	G	FG
Ovenbird	OVEN	<i>Seiurus noveboracensis</i>	G	GG
Palm Warbler*	PAWA	<i>Dendroica palmarum</i>	G	FG
Tennessee Warbler	TEWA	<i>Vermivora peregrina</i>	G	FG
Townsend's Warbler †	TOWA	<i>Dendroica townsendi</i>	CT	FG
Wilson's Warbler	WIWA	<i>Wilsonia pusilla</i>	G	FG

Yellow Warbler †	YEWA	<i>Dendroica petechia</i>	S	FG
Yellow-rumped Warbler	YRWA	<i>Dendroica coronata</i>	CT	FG
Chipping Sparrow	CHSP	<i>Spizella passerina</i>	CT	GG
Clay-colored Sparrow	CCSP	<i>Spizella pallida</i>	S	GG
Dark-eyed Junco	DEJU	<i>Junco hyemalis</i>	G	GG
Fox Sparrow*	FOSP	<i>Passerella iliaca</i>	G,S	GG
LeConte's Sparrow*	LCSP	<i>Ammodramus lecontei</i>	G	GG
Lincoln's Sparrow	LISP	<i>Melospiza lincolni</i>	G	GG
Savannah Sparrow †	SASP	<i>Passerculus sandwichensis</i>	G	GG
Swamp Sparrow*	SWSP	<i>Melospiza georgiana</i>	G,S	GG
Vesper Sparrow*	VESP	<i>Poocetes gramineus</i>	G	GG
White-crowned Sparrow †	WCSP	<i>Zonotrichia leucophrys</i>	S	GG
White-throated Sparrow	WTSP	<i>Zonotrichia albicollis</i>	G	GG
Rose-breasted Grosbeak	RBGR	<i>Pheucticus ludovicianus</i>	DT	FG
Western Meadowlark †	WEME	<i>Sturnella neglecta</i>	G	GG
Red-winged Blackbird	RWBL	<i>Agelaius phoeniceus</i>	W	GG
Rusty Blackbird*	RUBL	<i>Euphagus carolinus</i>	S,CT	GG
Western Tanager	WETA	<i>Piranga ludoviciana</i>	CT	FG
Fringillidae				
American Goldfinch*	AMGO	<i>Carduelis tristis</i>	S,DT	FG
Evening Grosbeak*	EVGR	<i>Coccothraustes vespertinus</i>	CT,DT	GG
Hoary Redpoll*	HORE	<i>Carduelis hornemanni</i>	G,S	FG
Pine Grosbeak †	PIGR	<i>Pinicola enucleator</i>	CT	FG
Pine Siskin	PISI	<i>Carduelis pinus</i>	CT	FG
Purple Finch	PUFI	<i>Carpodacus purpureus</i>	CT	GG
Red Crossbill	RECR	<i>Loxia curvirostra</i>	CT	FG
White-winged Crossbill	WWCR	<i>Loxia leucoptera</i>	CT	FG
Hirundinidae				
Tree Swallow †	TRSW	<i>Tachycineta bicolor</i>	A	AI
Muscicapidae				
Golden-crowned Kinglet	GCKI	<i>Regulus satrapa</i>	CT	FG
Ruby-crowned Kinglet	RCKI	<i>Regulus calendula</i>	CT	FG
Mountain Bluebird †	MOBL	<i>Sialia currucoides</i>	A	AI
Townsend's Solitaire †	TOSO	<i>Myadestes townsendi</i>	G	AI
American Robin	AMRO	<i>Turdus migratorius</i>	S,CT,DT	GG
Hermit Thrush	HETH	<i>Catharus guttatus</i>	G	GG
Swainson's Thrush	SWTH	<i>Catharus ustulatus</i>	S	FG
Varied Thrush †	VATH	<i>Ixorius naevius</i>	CT	GG
Paridae				
Black-capped Chickadee	BCCH	<i>Parus atricapillus</i>	A	FG
Boreal Chickadee	BOCH	<i>Parus hudsonicus</i>	A	FG

Picidae

Black-backed Woodpecker	BBWO	<i>Picoides arcticus</i>	A	BG
Downy Woodpecker	DOWO	<i>Picoides pubescens</i>	A	BG
Hairy Woodpecker	HAWO	<i>Picoides villosus</i>	A	BG
Northern Flicker	NOFL	<i>Colaptes auratus</i>	A	GG
Pileated Woodpecker	PIWO	<i>Dryocopus pileatus</i>	A	BG
Three-toed Woodpecker	TTWO	<i>Picoides tridactylus</i>	A	BG
Yellow bellied Sapsucker	YBSA	<i>Sphyrapicus varius</i>	A	BG

Scolopacidae

Common Snipe	COSN	<i>Gallinago gallinago</i>	G	PR
Lesser Yellowlegs †	LEYE	<i>Tringa flavipes</i>	G	PR
Greater Yellowlegs	GRLE	<i>Tringa melanoleuca</i>	G	PR
Solitary Sandpiper	SOSA	<i>Tringa solitaria</i>	G	PR
Spotted Sandpiper †	SPSA	<i>Actitis macularia</i>	G	GG

Sittidae

Red-breasted Nuthatch	RBNU	<i>Sitta canadensis</i>	A	BG
White-breasted Nuthatch	WBNU	<i>Sitta carolinensis</i>	A	BG

Troglodytidae

House Wren*	HOWR	<i>Troglodytes aedon</i>	A	GG
Sedge Wren*	SEWR	<i>Cistothorus platensis</i>	A	GG
Winter Wren	WIWR	<i>Troglodytes troglodytes</i>	A	GG

Tyrannidae

Alder Flycatcher	ALFL	<i>Empidonax alnorum</i>	S	AI
Eastern Kingbird †	EAKI	<i>Tyrannus tyrannus</i>	S,DT	AI
Hammond's Flycatcher †	HAFL	<i>Empidonax hammondi</i>	CT	AI
Least Flycatcher	LEFL	<i>Empidonax minimus</i>	S,DT	AI
Western Wood Pewee	WWPE	<i>Contopus sordidulus</i>	CT	AI
Yellow-bellied Flycatcher	YBFL	<i>Empidonax flaviventris</i>	G	AI

Vireonidae

Philadelphia Vireo	PHVI	<i>Vireo philadelphicus</i>	DT	FG
Red-eyed Vireo	REVI	<i>Vireo olivaceus</i>	S,DT	FG
Solitary Vireo	SOVI	<i>Vireo solitarius</i>	CT	FG
Warbling Vireo †	WAVI	<i>Vireo gilvus</i>	S,DT	FG

^a A = cavity, CT = coniferous tree, DT = deciduous tree, G = ground, S = shrub,

W = vegetation above-water.

^b AI = aerial insectivore, BG = bark glean, FG = foliage glean, GG = ground glean, HD = high dives, PR = probes.

† Species unique to Alberta.

* Species unique to Saskatchewan.