PROCESSES UNDERLYING NEST PREDATION BY INTRODUCED RED SQUIRRELS (Tamiasciurus hudsonicus) IN THE BOREAL FOREST OF NEWFOUNDLAND

KEITH P. LEWIS

PROCESSES UNDERLYING NEST PREDATION BY INTRODUCED RED SQUIRRELS (*Tamiasciurus hudsonicus*) IN THE BOREAL FOREST OF NEWFOUNDLAND

by

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ABSTRACT

Predator-prey relationships are an important element of population and ecosystem dynamics, and influence the evolution of phenotypic traits, life-history strategies, and behaviour. Predation of songbird nests has been intensively studied from these perspectives, and implicated in declining songbird populations, although results vary among studies. However, few studies have explored ecological mechanisms that could influence nest predators. Red squirrels (*Tamiasciurus hudsonicus*) are an important nest predator throughout their range, and have been introduced to the boreal forest of Newfoundland. Newfoundland is an ideal system for studying nest predation due to the low habitat and nest predator diversity relative to the rest of the boreal forest. Furthermore, Newfoundland presents an opportunity to test the influence of introduced species on a boreal ecosystem.

Within a predator assemblage, some predators have stronger interactions with their prey than others. I showed that exclusion of red squirrels caused a significant decline in nest predation, especially on ground nests. Unlike other regions of North America, there is no compensatory predation by other predators, i.e. red squirrels are the dominant nest predator. At a landscape level, red squirrel abundance and habitat use are influenced by gaps in the forest canopy created by the processes of disturbance and succession. Herbivory by introduced moose (*Alces alces*) and snowshoe hare (*Lagopus americana*), alters the vegetation in these gaps, indirectly influencing red squirrel predator avoidance behaviour. The result is substantially lower nest predation in gaps than in adjacent forest as reflected by patterns of red squirrel abundance. Finally, in an experiment testing multiple hypotheses, I found that nest predation was modestly influenced by red squirrel density but not nest concealment. I also tested a foraging theory based model of nest predation. This model predicts that variations in predator type, nest defense, alternate food for nest predators, and nest location influence nest predation, but I found that only supplemental food influenced nest predation.

This work demonstrates that understanding nest predation requires a knowledge of the nest predator assemblage and interactions therein, the mechanisms by which large scale ecological processes and interactions indirectly influence nest predator behaviour, and nest predator density and foraging ecology.

For Catherine

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1.0 Introduction and Overview

Predator-prey relationships are among the most important areas of study in ecology. These relationships are critical for understanding population and ecosystem dynamics (Lima 1998, Sih et al. 1998), as well as evolution of phenotypic traits (Endler 1986), life-history strategies (Lack 1968, Martin 1995, Bosque and Bosque 1995), and behaviour (Lima and Dill 1990, Lima 1998). Nest predation is the primary cause of nesting failure among passerine birds across a wide diversity of species, habitats, and geographic locations (Lack 1954, Ricklefs 1969, Martin 1993a). Nest predation has been studied extensively in terms of ecological patterns and processes, as well as evolutionary consequences and adaptations. Many studies have searched for ecological correlations, such as landscape features, of nest predation (reviews in Paton 1994, Andrén 1995, Bender et al. 1998, Söderström et al. 1998, Söderström 1999), while others have examined factors that influence inter-and intra-specific patterns of nest-site selection (Martin 1988a, 1988b, 1993a, 1993b, 1996, Marini 1997, Reitsma and Whelan 2000). Many other ecological factors (e.g. density of nests, predator abundance) that influence nest predation have been explored, but have individually received little attention.

Ecological studies of nest predation have largely focused on the influence of habitat edge and fragment size on patterns of avian nest predation (Paton 1994, Andrén 1995, Bender et al. 1998, Söderström et al. 1998, Söderström 1999), but often with little mechanistic understanding (Murica 1995). Increased nest predation at habitat edges or habitat fragments can result from many factors but is often attributed to increased nest predator species richness or a behavioural, functional, or numerical predator response (Dijack and Thompson 2000, Chalfoun et al. 2002). While highly attractive due to its simplicity and obvious conservation implications, increased nest predation at habitat edges seems to occur in ecosystems where disturbance and patchiness are naturally low but have been fragmented by human activity (Schmiegelow and Hannon 1993, Tewksbury et al. 1998), e.g. temperate deciduous forests fragmented by agriculture in mid-western North America (Andrén 1995) or tropical forests (Söderström 1999). Results from studies in other regions examining the influence of landscape on nest predation are equivocal (Andrén 1995), and may make little sense in naturally fragmented habitats (Tewksbury et al. 1999) such as the boreal forest.

A second approach has examined the role of nest-site selection at both patch and site scales, and dispersion in relation to other nests, as evolutionary adaptations to nest predation. Martin and Roper (1988) found that Hermit Thrushes (*Catharus guttatus*) selected nest-sites in patches with a large number of other potential nest sites. Individual nest-site characteristics such as nest concealment can also influence nest predation (Martin 1993a, Götmark et al. 1995) but results are equivocal (Filiater et al. 1994, Cresswell 1997). Similarly, large numbers of potential nest sites may decrease predation because a predator must search more potential nest-sites (Martin 1993a, Reitsma and Whelan 2000), promoting the partitioning of nests in both horizontal and vertical space (Martin 1996, Reitsma and Whelan 2000) and time (Major et al. 1994).

In a complex predator-prey relationship like nest predation, many factors influence observed patterns, although they have not been as intensively studied as habitat edges/fragmentation or nest-site selection. For instance, some birds actively defend their nests (Cresswell 1997, Schmidt et al. 2001a), and this can influence nest-site selection (Cresswell 1997) or life history traits (P. Gallo pers. comm.). Birds can also mob or distract predators by feigning injury (Martin 1992). The presence of parent birds at the nest may deter predators (i.e. passive defense, Schmidt 1999) or parents may avoid the nest when predators are in close proximity (Martin 1992). Indirect effects such as apparent competition (i.e. competition for enemy free space) can also influence nest predation (Hoi and Winkler 1994), and nest predators may respond in a density-dependent (Reitsma 1992, Schmidt and Whelan 1999) or frequency-dependent manner (Marini and Weale 1997). Alternately, nest predation may be largely the result of incidental predation by predators foraging for primary prey (Vickery et al. 1992a, Schmidt et al. 2001b).

Studies relating nest predator abundance to nest predation have only recently appeared (e.g. Zanette and Jenkins 2000, Rodewald and Yahner 2001, Patten and Bolger 2003). Mechanisms underlying these patterns vary but can be related to food and climate . For example, nest predation in arctic systems seems to be largely driven by the amount of alternate prey for nest predators (e.g. Bêty et al. 2001). Food and climate can alter both parental bird and nest predator behaviour and influence predation rates (Schmidt 1999, Morrison and Bolger 2002). Beyond simple numerical responses, not all predators have equivalent impact on prey populations (Schmidt et al. 2001a), and some clearly dominate the nest predator assemblage (Savidge 1987). Factors that influence nest predators' relationships with their own predators will clearly influence patterns of nest predators, especially if they are small mammals. Herbivores can exert a large influence on vegetation structure (Naiman 1988), which in turn, can indirectly effect both avian assemblages (Casey and Heing, Dobkin et al. 1998) and nest predation (Martin and Joron 2003).

1.1 INTRODUCED SPECIES

Although the primary focus of this thesis is nest predation, it is also an investigation of the direct and indirect effects of introduced red squirrels (*Tamiasciurus hudsonicus*) and other introduced species on nest predation in a boreal forest, island system. The ecological and economic influences of introduced species are enormous (Williamson 1996, Pimentel et al. 2000), and the rate at which species are introduced to new areas has rapidly increased in the last few hundred years due to human activities (Elton 1958, Carlton and Geller 1993, Lodge 1993a, Lövel 1997). Introduced species have caused more species extinctions than any other human factor except perhaps land use change (D' Antonio and Vitousek 1992), and are contributing to a rapid homogenization of the earth's biota (Lodge 1993b). The influence of introduced species is often profound on islands (e.g. Elton 1958), often contributing to an "ecological meltdown" (Simberloff and Van Holle 1999). Little work has been done to assess the ecological impacts of introduced species on the ecology of Newfoundland.

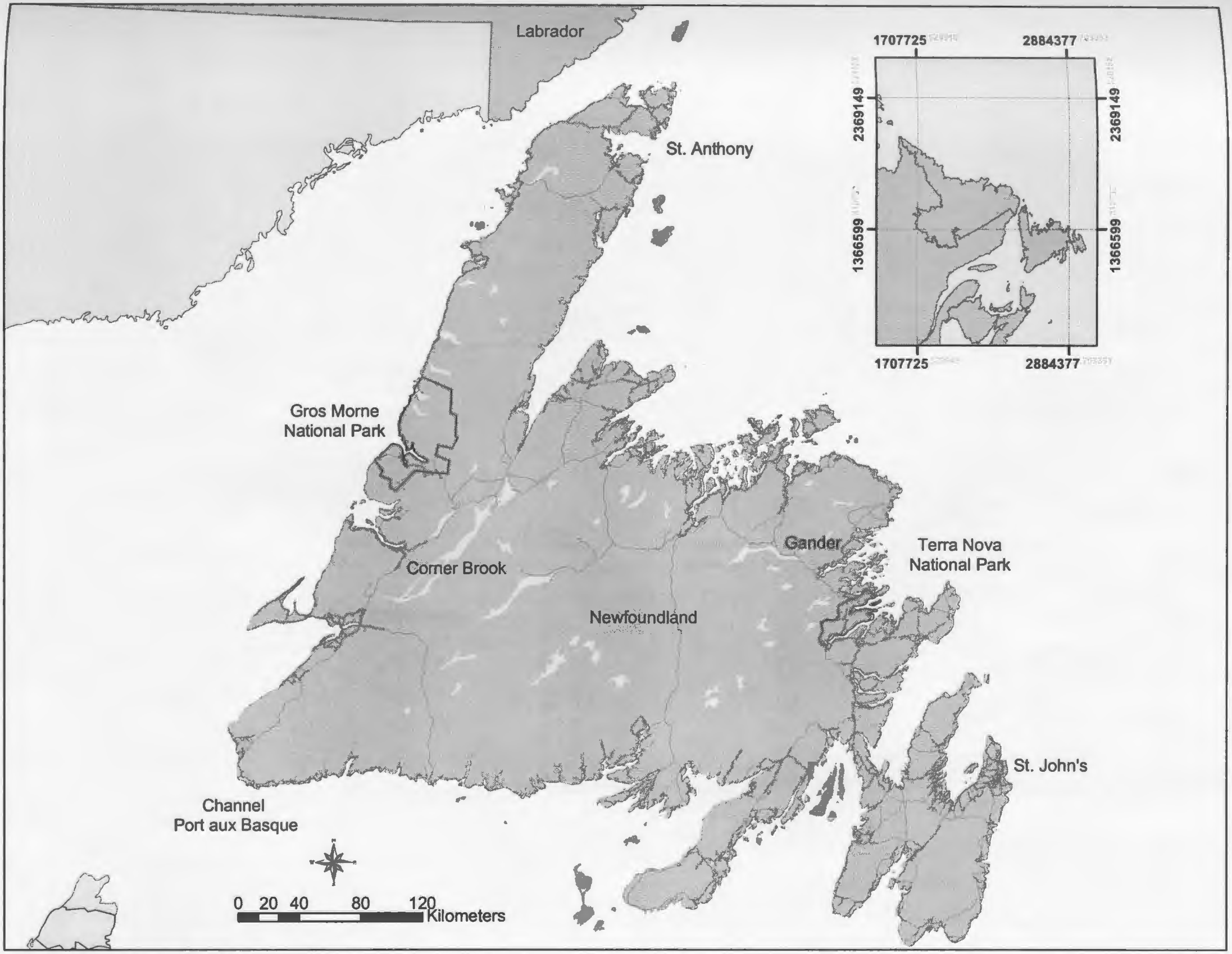
Many species have been introduced to Newfoundland since European colonization, and many are now widespread across the island. Those species that are adapted to the boreal forest such as moose (*Alces alces*), snowshoe hare (*Lepus americanus*), red squirrels (*Tamiasciurus hudsonicus*), and masked shrew (*Sorex cinereus*) now dominate the native biota (Dodds 1983). Moose populations and demography are well monitored, but those of other species are not, and their cumulative impact on the native biota is not known.

Of particular concern for nest predation are red squirrels which were introduced twice to Newfoundland in 1963 and 1964 (Payne 1976). The red squirrel rapidly expanded its range (Payne 1976, Goudie 1978) and is now found in most forested areas on the island. The red squirrel is an arboreal rodent, native to the boreal forest (Gurnell 1987). Red squirrels prefer mature forest and feed primarily on conifer cones (Smith 1968a, Smith 1968b, Rusch and Reeder 1978) but also utilize fungus, vegetative and reproductive buds (Smith 1968a). Given the ability of introduced species to alter ecosystems and the success of the red squirrel in Newfoundland, it is critical to understand its influence on different aspects of the ecosystem. Unfortunately, little information exists on red squirrels in Newfoundland. Red squirrels can severely and negatively influence cone crops through cone depredation (West 1989, English 1998, K. Tulk, pers.com.). Red squirrels play a large role in nest predation in Newfoundland (Lewis 1999, Lewis and Montevecchi 2001), and in other parts of their range (e.g.

Tewksbury et al. 1998, Willson et al. 2003, Martin and Joron 2003), perhaps because breeding seasons of red squirrels and birds overlap (Anderson and Boutin 2002). Although the influence of red squirrels on avian populations remains largely unknown, it may have contributed to the declines in the Newfoundland Red Crossbill (*Loxia curvirostra*; Benkman 1993). Population parameters of red squirrels have only been measured in Terra Nova National Park (TNNP) during 1994 and 1995 (Reynolds (1997), and red squirrels in pure balsam fir forests have not been studied, though they may be less abundant than in black spruce habitat (Wren 2001). A combination of a low species and landscape diversity, one primary predator, and many introduced species make Newfoundland an ideal system for exploring factors that influence nest predation.

1.2 A BRIEF OVERVIEW OF THE ECOLOGY OF NEWFOUNDLAND

The island of Newfoundland, situated off the coast of eastern Canada, is the world's sixteenth largest island (Fig. 1.1). Newfoundland has been isolated from the rest of the boreal forest since the last glaciation about 10,000 years ago, which removed much of the island's soil to the continental shelf (South 1983). The island's climate, except for the interior, is maritime, and strongly influenced by the Labrador Current, and the moderating influence of the ocean. The climate is characterized by mild to warm summers, cold but not severe winters, late springs, and frequent high winds. The island can be broadly categorized as having nine ecoregions, but climate, geology, and disturbance all contribute to an extremely heterogeneous landscape, that differs from



Labrador
St. Anthony
1707725
2884377
2369149
1366599
1707725
2884377
2369149
1366599
Gros Morne National Park
Corner Brook
Gander
Terra Nova National Park
Newfoundland
St. John's
Channel Port aux Basque
0 20 40 80 120 Kilometers

Fig. 1.1. The island of Newfoundland.

nearby parts of the Canadian mainland (Bergerud 1983). Approximately 56 % of Newfoundland is forested, 20 % heathlands (i.e. barrens), and 24 % wetlands and open water. Less than 1% of the land is urban or agricultural. Balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) dominate the forests of western and eastern Newfoundland respectively (Meades 1990). Insect, wind, and gap disturbance dominate western Newfoundland while fire is the main disturbance agent in other areas (Meades and Moores 1989). Clearcutting for pulp and paper is the main form of anthropogenic disturbance.

The biota of Newfoundland are also distinct from neighboring land masses. Many plant and animal species reach the limits of their northern or southern distributions (Meades 1990). While many avian species are found on the island (Mactavish et al. 2002), the richness of common forest birds is markedly lower than other parts of eastern North America including Nova Scotia (Montevecchi and Tuck 1987). In addition, only 14 native mammals, including nine carnivores, were found on the island at the time of European colonization, less than half of what is found in nearby Cape Breton Island and Labrador. However, many avian species and nine mammals are distinct enough to be considered a subspecies (Bergerud 1983, Dodds 1983, Montevecchi and Tuck 1987).

1.3 ARTIFICIAL NESTS

There are three main methods for studying nest predation: search for and monitor real nests (Martin and Guepel 1993), develop an index of breeding productivity (Vickery et al. 1992b, Gunn et al. 2000), and artificial nests. Throughout this thesis, I rely on artificial nests to study the influence of introduced species on nest predation in Newfoundland. Artificial nests have been extensively used to study nest predation because they can offer a large degree of experimental control and often require far less labour than searching for real nests.

However, artificial nest studies have substantial limitations and have been criticized for not providing a reliable index of predation on natural nests (e.g. Willebrand and Marcstöm 1988, Ortega et al. 1998), though in some areas, trends in nest predation are similar between real and artificial nests (Wilson et al. 1998). Most researchers assume that relative rates of nest predation are similar between real and artificial nests, but predation rates between nest types can differ among study sites (Davidson and Bollinger 2000), and nest predators differentially favor different nest types (Bueer and Hamilton 2000). Also, nest parasitism may be a primary factor responsible for nest failure but is not measured with artificial nests (Wilson et al. 1998).

The most obvious difference between real and artificial nests is lack of parental and nestling activity and all other associated cues that may indicate a nest's location. For example, raptors are important predators during the nestling stage but are apparently not a major factor during incubation (Liebezeit and George 2002). Therefore, artificial nests are likely a better measure of predation during the incubation stage.

Another reason for the discrepancy between predation of real and artificial nests is the type of egg used. Japanese Quail eggs may not be appropriate for artificial nest studies if small mammals are the major nest predator (e.g. Roper 1992, Haskell 1995). However, other researchers have shown that small mammals can prey on Japanese Quail eggs (Craig 1998), and Blight et al. (1999) found that Keen's mouse (*Peromyscus keeni*) can penetrate eggs larger than themselves. Egg size can influence predation rates between habitat types (Lindell 2000), but not in all circumstances (Lewis and Montevecchi 1999, DeGraaf 1999). In Newfoundland forests, this bias is probably minimal because the few species of small mammals other than red squirrels are usually found in low densities, and nest predation levels did not change when using smaller Chinese Painted Quail (*Xexcalfactoria chinensis*) eggs (Lewis and Montevecchi 1999).

A problem with both real and artificial nest studies is that identification of predators from egg remains is highly unreliable (Marini and Melo 1998, Larivière 1999). In Newfoundland, there are few predators, so the chance of misidentifying a predator is reduced. Another bias in both real and artificial nest studies is human scent. Davidson and Bollinger (2000) showed that artificial nests of grass had levels and patterns of nest predation that more closely corresponded to real nests than artificial nests of wicker. Scent trails may also increase predation (Whelan et al. 1994, but see Skagen et al. 1999).

While studies with real nests are clearly preferable, findings from artificial nests studies can be valuable in some circumstances. First, relative to most forested areas in North America, this study was conducted in an area with a small nest predator assemblage. The concerns about misidentifying predators are less, and differences in predation levels between real and artificial nests may not be great (Martin and Joron

2003). Second, attempts to find real nests in Newfoundland forests have yielded extremely small sample sizes (Lewis 1999). It is better to conduct a study and interpret the findings cautiously given known biases than to not conduct the study at all. Finally, given that artificial nests lend themselves to experimental designs, they are extremely useful in testing novel hypotheses and investigating mechanisms underlying nest predation that can latter be validated by studies using other techniques (Schmidt et al. 2001b). A possible solution when nests are either very difficult to locate or large groups of nest searchers are not available, would be to conduct similar experiments but determine breeding productivity, rather than nesting success, using methods such as the Vickery-Gunn index (Gunn et al. 2000).

Despite the many criticisms of nest predation studies using artificial nests, there are many theoretical and conservation questions that would be extremely difficult to study with real nests. Marini and Schmidt conducted a series of experiments that demonstrate the continued utility of artificial nests. Marini et al. (1995) examined four alternate, non-exclusive hypotheses that have been suggested as explanations for increased nest predation at edges. Marini (1997) found support for the predation/diversity hypothesis, i.e. species poor communities should experience higher levels of nest predation than species rich communities, at the landscape level. Marini and Weale (1997) examined density- and frequency-dependent predation and showed that predation rates depend on an interaction between the density and diversity of various prey. In a series of papers, Schmidt examined how apparent competition structures avian communities (Schmidt and

Whelan 1998) and investigated factors that influence density-dependent predation (Schmidt and Whelan 1999). He also suggested the use of foraging theory as a conceptual framework for nest predation (Schmidt 1999), explored the functional role of different nest predators (Schmidt et al. 2001a), and factors that influence incidental nest predation (Schmidt et al. 2001b). The experiments conducted by these researchers demonstrate the utility of artificial nests to test novel hypotheses, especially at the community level. This thesis follows their examples.

1.4 THESIS OUTLINE

This thesis takes a mechanistic approach and investigates processes that influence nest predation patterns by introduced red squirrels. In Chapter 2, I examined the role of red squirrels within the nest predator assemblage. In Chapter 3, I explored how landscape processes and interactions influence red squirrel behaviour and patterns of nest predation. Finally, in Chapter 4, I simultaneously tested hypotheses of nest predator density and nest concealment with a model of nest predation based on foraging theory.

1.4.1 CHAPTER 2

Although many animals prey on birds eggs and nestlings, the influence of different species varies (Schmidt et al. 2001a). In many systems, certain predators depredate a disproportionate number of nests (Savidge 1987). However, the strength of the influence that primary predators exert on avian assemblages varies among systems, suggesting that a diverse nest predator assemblage can compensate for the absence of primary nest predators (Reitsma et al. 1990). A lack of understanding of predator importance likely contributes to variation among nest predation studies, and hampers theoretical development. This chapter assesses the influence of introduced red squirrels on patterns of nest predation in Newfoundland. I introduce and test two mutually exclusive hypotheses, suggest an additive/compensatory framework for examining the role of nest predators, and speculate under what conditions these alternate patterns occur.

1.4.2 CHAPTER 3

That vegetation structure and diversity, and previous disturbance and successional patterns, influence avian assemblages is well established (MacArthur and MacArthur 1961, Helle and Niemi 1996). Yet, with few exceptions, ornithologists have conducted their research as though the structure and diversity of the local vegetation were not influenced by disturbance and herbivory. Herbivores can dramatically influence successional pathways, plant composition, structure and production (Naiman 1988), especially where they are not native (Chapuis et al. 1994), maintained at artificially high levels (Dobkin et al. 1998, Bock and Bock 1999, McLaren et al. in press), and/or lack predators (Crête et al. 2001). By altering vegetation, herbivores can also indirectly influence the behaviour of nest predators through modifying their foraging decisions (Brown 1988, Lima and Dill 1990), potentially providing a mechanistic explanation for observed patterns. A comprehensive framework linking these disparate areas of disturbance/succession, plant-herbivore interaction, bird habitat selection, and predator-prey interactions is lacking. This chapter addresses this shortcoming and tests this model using red squirrels on post-disturbance sites in Newfoundland.

1.4.3 CHAPTER 4

Many studies of edge effects and habitat fragmentation assume that landscape changes promotes an increase in predator richness, or a behavioural, functional, or numerical predator response (Chalfoun et al. 2002). Nevertheless, the few studies that quantify predator populations often use techniques that may not reliably estimate density. Other studies have explored the implications of nest patch and nest site selection, generating hypotheses such as the potential-prey and nest concealment hypotheses (Martin 1993a). These approaches have met with equivocal success, likely due to the multiple factors that influence nest predation. Despite a rich literature, foraging theory has only recently been applied to the study of nest predation (Schmidt 1999). Schmidt proposed that factors influencing predator-prey interactions, such as predator type, alternate food, and nest characteristics, could explain intraspecific variation in nest predation. In Chapter 4, I use red squirrels to simultaneously test the nest predator density and nest concealment hypotheses with Schmidt's model of nest predation.

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1.6 STATEMENT OF AUTHORSHIP

I conducted this research independently but under the supervision of Dr. William Montevecchi and with the support of my committee members, Drs. Luise Hermanutz, Brian McLaren, and Ian Warkentin. I was responsible for the design and execution of the field studies. I was assisted in the field work by Crispen Jenkins in 2000 and Marc Linehan in 2001-02, and numerous volunteers, who carried out fieldwork under my supervision and followed my guidelines and protocols. Handling of red squirrels was conducted with the approval of Memorial University's Institutional Animal Care Committee (Protocol Number 00-04-WM).

I collated, entered, and analysed all data. In addition, I interpreted all the results and wrote the manuscripts that constitute the chapters of this thesis. I have revised the manuscripts based on the advice and comments of my supervisor, supervisory committee, trusted colleges, and journal reviewers. Chapter 2, Lewis K.P. and W. A. Montevecchi, The introduced red squirrel as the dominant nest predator in the boreal forest of Newfoundland, has been submitted to the Canadian Journal of Zoology. Chapter 3, Lewis, K.P. and W. A. Montevecchi.,The influence of disturbance and herbivory on nest predation through their indirect effects on red squirrels, has been submitted to Ecography. Chapter 4, Lewis, K.P. and W. A. Montevecchi, Mechanisms underlying nest predation by introduced red squirrels (*Tamiasciurus hudsonicus*) in the Newfoundland boreal forest, has been submitted to the Journal of Animal Ecology. Differences in formatting among chapters reflect differences in styles among the different journals.

2.0 The introduced red squirrel as the dominant nest predator in the boreal forest of Newfoundland

2.1 ABSTRACT

Nest predation has been extensively studied, but the influence of nest predator assemblages on nest predation has received little attention. Variation in the number and characteristics of predators can greatly influence patterns of nest predation. I tested the Dominant Predator and Nest Predator Diversity hypotheses which make opposite predictions; removal of the primary nest predator(s) will decrease nest predation (i.e additive predation), or have no influence on nest predation (i.e. compensatory predation) respectively. These hypotheses were tested in a relatively simple system, the boreal forest on the island of Newfoundland where introduced red squirrels (*Tamiasciurus hudsonicus*) are the primary nest predator. To test the influence of removing red squirrels on patterns of nest predation, I conducted an artificial nest experiment in black spruce (*Picea mariana*) and balsam fir forests (*Abies balsamea*) during 2001 and 2002. Nests were placed in exclosures, half of which excluded only red squirrels, while half permitted nest access by all predators. Nests were depredated mostly by red squirrels and Gray Jays (*Perisoreus canadensis*). Eliminating predation by red squirrels significantly lowered nest predation in both forest types in both years, supporting the Dominant Predator Hypothesis. Introduced red squirrels appear to have an additive effect on levels of nest predation in Newfoundland, especially on ground nests. Both hypotheses have been supported by other studies. Discriminating between these hypotheses is important for effective management of predators and avian populations, as well as and developing nest predation theory by understanding the functional role of different predators

Keywords additive predation, boreal forest, dominant predator, predator removal, introduced red squirrel

2.2 INTRODUCTION

Predation is a key factor influencing patterns in natural systems as well as community structure (Sih et al. 1998). The functional role of different predators, or the interaction strengths between predator and prey, are critical to understanding the influence of predation within a system (Paine 1992, Schmidt 2001a, Chalcraft and Resetarits 2003). Nest predation is the primary cause of nesting failure among passerine birds across a wide diversity of species, habitats, and geographic locations (Lack 1954, Rickleffs 1969, Martin 1993). Nest predation has been studied extensively in terms of ecological patterns and processes (Paton 1994, Söderström et al. 1998), as well as evolutionary consequences and life history strategies (Martin 1995). Although rarely investigated, variation in the size and composition of the nest predator assemblage can profoundly affect the ecological patterns (Greenwood 1986, Miller and Knight 1993), and evolutionary consequences (Bosque and Bosque 1995) of nest predation. A single predator species, or suite of species (primary predator(s) hereafter), can be primarily responsible for nest predation (Savidge 1987). Alternatively, the absence of primary predator(s) may have little influence on patterns of nest predation. For instance, other predators (secondary predators hereafter) might not be important nest predators but could cause high levels of nest predation in the absence of primary predators (Reitsma et al. 1990). A lack of understanding of the relative contribution of each predator likely contributes to variation among nest predation studies, and hampers theoretical development.

Research by Reitsma et al. (1990) found that removal of the primary predators, red squirrels (*Tamiasciurus hudsonicus*) and eastern chipmunks (*Tamias striatus*) did not significantly change levels of nest predation due to compensation by other nest predators. This research suggests the Nest Predator Diversity Hypothesis; if secondary predators are ineffective due some interaction with a primary predator species, then removal of the primary nest predator will not influence over all levels of nest predation. Interactions that could minimize the influence of secondary predators include competitive exclusion by the primary nest predator due to greater searching efficiency (Reitsma et al. 1990), a reduction in time spent searching for nests by the secondary predator due to intra-guild predation by the primary predator (Dion et al. 1999a, 1999b, Lewis and Montevecchi, submitted), or suppressed populations of secondary predators (Rogers and Caro 1998). In any case, upon removal of the primary predator, compensatory predation will occur as secondary predator species increase their depredation of nests, i.e. predation levels will not change in the primary predator's absence. An alternative is the Dominant Predator Hypothesis; if secondary predator species are simply not present, are ineffective nest predators, or do not have access to nests due to location, then removal of the primary nest predator species should greatly decrease nest predation. This suggests that nest predation by the primary predator species is additive, i.e. predation by the primary predator increases predation levels above what they would be in the predator's absence (Fig. 2.1).

Although there have been dozens of predator removal studies (Beauchamp et al. 1996, Côté and Sutherland 1996, Newton 1998), most remove multiple predator species

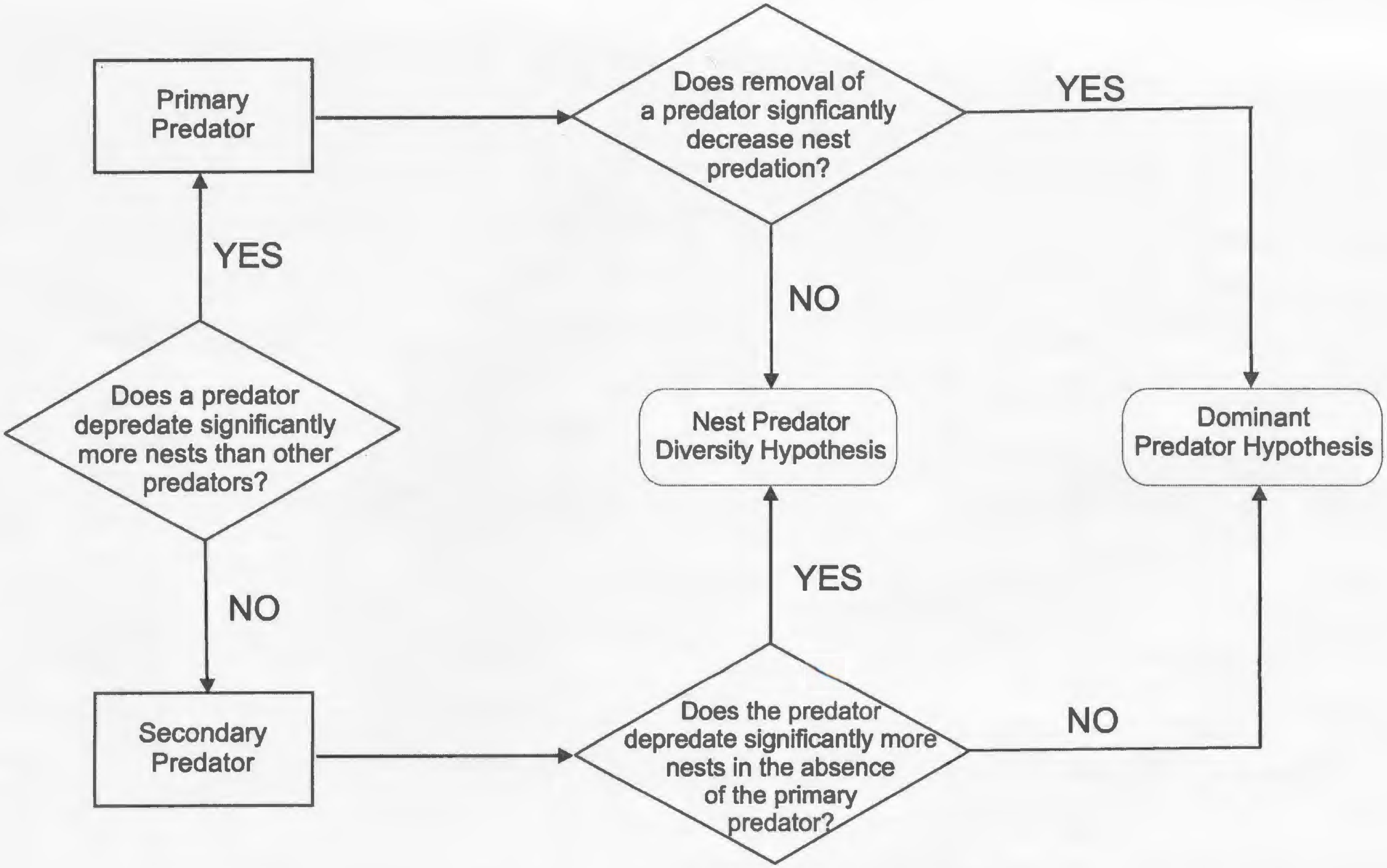

Fig. 1. Conceptual framework for the Dominant Predator/Nest Predator Diversity Hypotheses

preventing inference to be made about the effect of individual predator species. Many studies do not test these hypotheses in an *a priori* fashion, have been conducted on ground nesting game species, and use some form of predator control that alters species interactions (e.g. large exclosures, traps, lethal removals, etc.). I tested the Dominant Predator and Nest Predator Diversity hypotheses for tree- and ground-nesting song birds using artificial nests in the boreal forests of Newfoundland using small exclosures that eliminated the primary predator, the introduced red squirrel, but did not alter interactions among species.

The island of Newfoundland provides an ideal system to test nest predation hypotheses due to a limited predator assemblage (Dodds 1983) coupled with relatively few distinct types of habitat (Meades and Moores 1989). Also, agriculture is rare, comprising less than 1% of the landmass, and geographically restricted in Newfoundland so studies are not confounded by species like corvids whose populations tend to increase with human development (Andrén 1992, Bayne and Hobson 1997). Nest parasitism is not a concern because Brown-headed Cowbirds (*Molothrus ater*) are rare (Mactavish et al. 2003).

Red squirrels are important nest predators across most of their range, primarily the boreal and coniferous forests of North America (Bayne and Hobson 1997, Darveau et al. 1997, Tewksbury et al. 1998, Lewis 1999, Martin and Joron 2003, Willson et al. 2003), and may increase levels of nest predation primarily by depredating ground nests (Lewis 1999). The red squirrel (*Tamiasciurus hudsonicus*) was introduced to Newfoundland in

1963 (Payne 1976) and has invaded virtually all forested areas. Introduced species can have especially large impacts on the ecosystems that they invade (Elton 1958).

In this study, I first establish that introduced red squirrels are the primary nest predator on the island of Newfoundland. Then, by eliminating nest predation by red squirrels, I will test the Dominant Nest Predator and Nest Predator Diversity Hypotheses and whether the introduction of a single predator has additive or compensatory effects on nest predation. The Dominant Nest Predator Hypothesis predicts that removal of red squirrels will significantly decrease levels of nest predation, in this case, mostly on ground nests. In contrast, the Nest Predator Diversity Hypothesis predicts that there will be no change in levels of predation. I also consider the influence of the introduction of red squirrels on avian populations and diversity in the boreal forest of Newfoundland. Discriminating between these hypotheses is important for effective management of predators and avian populations, as well as developing nest predation theory by understanding the functional role of different predators

2.3 MATERIALS AND METHODS

In order to provide a more comprehensive test within Newfoundland of the Nest Predator Diversity Hypothesis and Dominant Predator Hypothesis, study sites were established in the two dominant forest types on the island of Newfoundland: black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Study sites in Terra Nova National Park (54° 00' W, 48° 30' N) in eastern Newfoundland were located in the North-central Subregion of the Central Newfoundland ecoregion (Meades and Moores 1989). This region is dominated by black spruce but balsam fir are commonly found on more fertile soils. White birch (*Betula papyrifera*), trembling aspen (*Populus tremulodies*), and alder (*Alnus* spp.) occur less commonly, whereas larch, (*Larix larcina*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) occur rarely throughout the park and this region. Peatlands, wetlands, and barrens are common (Power 2000). Sheep laurel (*Kalmia angustifolia*) is a dominant understory shrub, associated with black spruce forest and barrens. A diverse assemblage of vascular plants, moss, and lichens are found in this area. Fire, insects, wind, and a number of introduced herbivores, including moose (*Alces alces*), snowshoe hare (*Lagopus americanus*), and red squirrels, all influence the vegetation and diversity of these forests. Disturbance combined with the variable hydrogeology contribute to a highly varied and fragmented ecosystem (Power 2000).

Study sites in Gros Morne National Park (49° 40' W, 57° 45' N) were located in the Corner Brook Subregion of the Western Newfoundland Ecoregion, characterized by a rugged topography and generally nutrient rich soils (Meades and Moores 1989). Balsam fir and white birch are the dominate tree species, with lesser amounts of white spruce (*Picea glauca*) and black spruce. The latter is often found primarily on bedrock outcrops and poorly drained sites. Peatlands are less common than in Terra Nova National Park. Ericaceous shrubs are rare and heaths develop only in very small areas. Disturbances are similar to Terra Nova National Park except that defoliation by insects such as hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) is the dominant disturbance type rather than fire (Meades and Moores 1989).

2.3.1 NEST PREDATORS

Potential avian nest predators in Newfoundland include the Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and Gray Jay (*Perisoreus canadensis*). During six years of field work in these areas, only Gray Jays and Common Ravens were observed on the study sites (K. Lewis pers. obs.), but both were uncommon. Common Ravens were usually seen flying over the study sites; only once was a Common Raven seen in the forest. Potential native mammalian nest predators include black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), American marten (*Martes americanus*), short-tailed weasel (*Mustela erminea)*, and meadow vole (*Microtus pennsylvanicus*). Other introduced mammalian predators include red squirrel, mink (*Martes vison*), deer mouse (*Peromyscus maniculatus*), eastern chipmunk (*Tamias striatus*), boreal redback vole (*Clethrionomys gapperi*), and possibly masked shrew (*Sorex cineurus*, Dodds 1983). Deer mice occur in Gros Morne National Park and western Newfoundland (S. Gerrow and D. Snow pers. comm.), but do not yet occur in eastern Newfoundland (J. Gosse pers. comm.). Eastern chipmunks are slowly spreading north in western Newfoundland and are found as far north as Gros Morne National Park (K. Lewis pers. obs.). The boreal red-back vole was probably introduced to western

Newfoundland in 2000, but has not reached Terra Nova or Gros Morne National Parks (S. Gerrow and J. Gosse pers. comm.).

Additional nest predators have been found in other boreal studies, which usually have a far more diverse nest predator assemblages including other species of birds, chipmunks, mice, mustelids (e.g. striped skunk *Mephitus mephitus*, and Black-billed Magpie *Pica pica*, Bayne and Hobson 1997). Newfoundland lacks many potential nest predators common to other parts of North America including raccoon (*Procyon lotor*), striped skunk, gray squirrel *(Sciurus carolinensis*), wood rats (*Neotoma* spp.), opossums, (*Didelphis virginiana*), gray fox (*Urocyon cinereorgenteus*), badgers (*Taxidea taxus*), many small rodents, and snakes.

2.3.2 STUDY DESIGN

This study was conducted on six grids in mature black spruce stands in Terra Nova National Park in 2001. In 2002, three additional grids in Terra Nova National Park, and six grids in mature balsam fir stands in Gros Morne National Park were established. Grids were generally 200 x 100 m (2 ha) but one was 150 x 100 m (1.5 ha) due to the size of the forest stand. Stations on the grids were established at 50 m intervals in a 5 x 3 pattern. All grids were separated by at least 1 km but the distance was usually 5 km or greater. Three study sites were chosen to coincide with another study on red squirrel depredation of black spruce and balsam fir cones. Other sites were selected from GIS and aerial photographs, and subsequently ground-truthed to insure homogeneity of habitat.

Areas of insect defoliation, bogs, roads, cut blocks, power line corridors, scrub spruce, and other edges were avoided whenever possible although these forests are naturally highly fragmented. Study sites varied in terms of basal area, density, age, and ground cover of kalmia (K. Lewis unpubl. data), but are representative of the highly variable black spruce forests of Terra Nova National Park and balsam fir forests of Gros Morne National Park.

Like Reitsma et al. (1990), and other studies in the boreal forest (e.g. Darveau et al. 1997, Bayne and Hobson 1997), I used artificial nests. Natural bird nests are extremely difficult to locate in Newfoundland forests due to low density and difficult searching conditions. Despite the debate over their use, artificial nests may yield an index of actual nest predation (e.g. Wilson et al. 1998, Pärt and Wretenberg 2002), and nest predation has been shown to be similar between artificial and real nests in simple systems where red squirrels are the dominant predator (Martin and Joron 2003). Furthermore, artificial nests permit the investigation of mechanisms underlying nest predation in controlled experiments with adequate sample sizes (Schmidt et al. 2001b).

Unlike other studies (e.g. Reitsma et al. 1990, Schmidt et al. 2001a), I chose not to remove red squirrels from these study areas for two reasons. First, the effectiveness of removing sciurids through live trapping is questionable. Although Reitsma et al. (1990) and Schmidt et al. (2001a) intensively live trapped sciurids and smaller rodents respectively, some were still found on the study sites during the experiment. This could be due to either 1) the high colonization rates of sciurids (Price et al. 1986, S. Boutin pers. comm.), or 2) trap shy animals that were never removed. Second, complete removal of red squirrels requires daily trapping, and this was not logistically feasible on large numbers of widely separated, large-scale trapping grids. In addition, removal of red squirrels combined with constant human activity on the study sites due to trapping could bias the results by affecting the behaviour of other nest predators.

Instead of removing predators, I designed and built small cages (hereafter called exclosures, approximately 12 x 12 x 8 cm) out of hardware cloth (12 x 13 mm mesh) around artificial nests. As the experimental treatment (treatment exclosure), 5 holes (~ 24 x 26 mm) were cut in the exclosure; one in the middle of the top and one on each of the four sides. Holes were large enough that shrews, voles, and weasels can pass through, but not red squirrels (R. Cox pers. comm.). Birds, such as Gray Jays were able to prey on eggs in treatment exclosures. Others have used this technique of selectively excluding predators to examine additive and compensatory predation (Hamilton 2000). A bias in this design is that mink and larger predators might not be able to extract eggs from treatment nests. However, this bias should be minimal for several reasons. First, mink were not a factor in this study, as it was not conducted in riparian areas. Second, American marten are endangered in Newfoundland and are assumed to be too rare to have an effect at the landscape level for the purposes of this study (Power 2000). Third, although red fox and black bear would have a difficult time extracting eggs from treatment exclosures, the exclosures would have been moved, disturbed, or bent if attacked by these larger predators. Except for one nest, I did not observe any such occurrences. As a control, I constructed exclosures (control exclosures) of the same size but with larger holes (~ 5 x 6.2 cm) in the same locations as the treatment exclosures that make eggs accessible to all predators.

Small wicker baskets (~ 9 cm diameter x 3 cm deep) were used as artificial nests and placed in the exclosures with the edge of the nest ~ 1.5 cm from holes. Artificial nests were baited with Japanese Quail (*Coturnix japonica*) eggs (JQE), an appropriate sized egg for the nest predator assemblage in Newfoundland (Lewis and Montevecchi 1999), and a clay egg of comparable size tethered to the nest with snare wire. Clay eggs were of similar colour to the JQE, and small pieces of organic soil were added to the clay closely approximating a JQE in appearance. Eggs were placed in the nests near the holes in the exclosures to facilitate access by predators.

Exclosures were set out on the study grids on 10 and 12 June 2001 (81 nests), 9 to 10 June 2002 in Terra Nova National Park (127 nests), and 17 to 18 June 2002 in Gros Morne National Park (90 nests). A control or treatment exclosure was randomly assigned to each station. In addition, I randomly determined whether the exclosure was placed on the ground or in a tree (hereafter nest height) within 10 m of the station. Ground exclosures were placed under a tree, log, or in a patch of *Kalmia*. Tree exclosures were placed 2-4 m high on branches and secured with 1-2 black cable ties. Due to the conspicuousness of the exclosures, I did not go to great efforts to conceal them, but it is unlikely that they would be noticed by a human casually walking through the study area.

All nests were checked two weeks after being set out. A nest was considered depredated if any of the eggs were missing or had marks on them.

2.3.3 STATISTICAL ANALYSIS

Differences in predation on artificial nests were tested using logistic regression, a special form of the generalized linear model used for the analysis of binary or proportional response data with multiple explanatory variables (Agresti 1996), as is most appropriate for these data (Lewis 2004). To examine the influence of red squirrels on levels and patterns of nest predation, I used one- and two-way log-linear models (Agresti 1996). All analyses were performed using PROC GENMOD (SAS Institue 1989-96). Differences in deviance among model terms are reported as ΔG with the degrees of freedom as a subscript. For some analyses, I collapsed some categories or predators such as Gray Jay and unknown bird due to limited degrees of freedom. All results are reported as Type III analysis (analogous to adjusted sums of squares). I used a Bonferoni adjustment on $\alpha = 0.05$ when performing post-hoc analyses.

2.4 RESULTS

The number of nests depredated by each predator in both years and forest types are summarized in Appendix 2.1. In 2001, red squirrels depredated 13 of 23 nests and probably four others. Birds depredated four nests with two being confirmed as predation by Gray Jays. In 2002 in black spruce forests, red squirrels depredated 17 of 35 nests and probably three others. Birds depredated six nests with three being confirmed as predation by Gray Jays. In 2002 in balsam fir forests, red squirrels depredated 12 of 26 nests and probably two others. Birds depredated six nests with five being confirmed Gray Jays. In both forest types and years, red squirrels successfully depredated control nests but were unable to prey on treatment nests with one possible exception. Birds preyed on treatment nests with three of four avian attacks being on treatment nests in 2001 but only one of six in 2002. No other predators were detected in 2001, but there were two nests where the predator could not be identified. In 2002, eastern chipmunk, red fox, unidentified small mammals, and unidentified sciurids were detected in addition to seven nests where the predator could not be identified.

The number of depredated nests in black spruce forests was not independent of predator species in 2001 ($\Delta G_3 = 15.8$, $p = 0.0012$) or 2002 ($\Delta G_6 = 28.21$, $p < 0.0001$), and red squirrels depredated significantly more nests than the next most common predator in both years (2001: $\Delta G_1 = 9.01$, $p = 0.0027$; 2002: $\Delta G_1 = 10.82$, $p = 0.0010$, Bonferoni adjustment for multiple comparisons applied). In 2002 in balsam fir forests, the number of depredated nests was not independent of predator species ($\Delta G_7 = 24.31$, $p < 0.0010$), but red squirrels did not depredate significantly more nests than the next most common predator ($\Delta G_1 = 2.97$ $p = 0.0848$, Bonferoni adjustment for multiple comparisons applied, $n = 27$).

In 2001, control exclosures, especially those on the ground, experienced significantly greater levels of depredation than treatment exclosures ($\Delta G_1 = 9.18$, $p = 0.0024$; Table

2.1). The interaction between nest height and exclosure type, and the influence of nest height was not statistically significant ($\Delta G_1 = 0.05$, $p = 0.8205$; $\Delta G_1 = 1.29$, $p = 0.2552$, $n = 388$). In 2002, control exclosures again experienced significantly higher levels of predation than treatments in both black spruce ($\Delta G_1 = 27.41$, $p < 0.0001$) and balsam fir forests ($\Delta G_1 = 16.80$, $p < 0.0001$). The interaction between nest height and exclosure type, and the influence of nest height was not statistically significant in black spruce interaction: $\Delta G_1 = 1.18$, p 0.2777 , $n = 507$; nest height: $\Delta G_1 = 2.38$, $p = 0.1227$, $n = 252$) or balsam fir (interaction: $\Delta G_1 = 1.00$, $p = 0.3176$, $n = 424$; nest height: $\Delta G_1 = 0.72$, p 0.3972, $n = 589$) forests.

Nest predation was not independent of predators and nest height in any year or forest type (black spruce 2001: $\Delta G_6 = 18.94$, $p = 0.0043$; black spruce 2002: $\Delta G_9 = 20.57$, $p = 0.0147$; balsam fir 2002: $\Delta G_9 = 20.44$, $p = 0.0154$) with red squirrels depredating mostly control exclosures on the ground in all forest types and Gray Jays depredating mostly tree nests.

2.5 DISCUSSION

The predator exclosures were generally effective at selectively eliminating predation by red squirrels but not by other predators. The greater predation on control exlosures supports the Dominant Predator Hypothesis. These results suggests that the introduction of red squirrels to Newfoundland has had an additive effect by substantially increasing nest predation, especially on ground nesting birds.

Table 2.1. The proportion of depredated nests (nests depredated/total nests; percentage in parentheses) by exclosure type and location for 2001/2002 in black spruce and balsam fir forests.

		2001			2002		
Forest Type	Exclosure Location	Control	Treatment	Total	Control	Treatment	Total
black spruce	Ground	11/21 (52)	3/19 (15)	14/40 (35)	14/32 (44)	1/32 (3)	15/64 (23)
	Tree	7/21 (33)	2/20 (10)	9/41 (22)	16/32 (50)	4/31 (13)	20/63 (32)
	Total	18/42 (43)	5/39 (13)	23/81 (28)	30/64 (47)	5/63 (8)	35/127 (28)
balsam fir	Ground				14/23 (61)	2/24 (8)	16/47 (36)
	Tree				7/21 (33)	2/22 (9)	9/43 (21)
	Total				21/44 (48)	4/46 (11)	25/90 (28)

2.5.1 SUPPORT FOR THE DOMINANT PREDATOR OR NEST PREDATOR DIVERSITY HYPOTHESIS?

Dominant predators must first be established as a primary predator. Red squirrels were the primary predator and depredated more nests than any other species. Other species depredated nests but with the exception of Gray Jays, were not significant predators (Appendix 2.1). Red squirrels are a primary nest predator in much of the boreal and sub-boreal forests of North America (Darveau et al. 1997, Bayne and Hobson 1997, Tewksbury et al. 1998, Lewis 1999, Martin and Joron 2003, Willson et al. 2003) for many reasons. First, compared to other predators, the probability of a red squirrel finding a nest is high, since they occur in high densities relative to many other species and are found in virtually all forested habitat in Newfoundland and throughout their range (Rusch and Reeder 1978). Second, few forest songbird nests are inaccessible to a red squirrel. Third, aside from large corvids, few songbirds are capable of defending their nest once it has been detected by a red squirrel (W. Klenner pers. comm). Finally, the energetic benefits of depredating a nest are greater for a squirrel than for larger predators, and hence there is a greater motivation to search for nests..

The dramatic decrease in nest predation on the treatment exclosures, coupled with the large increase in predation at control exclosures by red squirrels, but not other predators, supports the Dominant Predator Hypothesis, indicating that nest predation by red squirrels is additive to that of other predators. The influence of red squirrels on nest predation can be both additive (Martin and Joron 2003), or compensatory (Reitsma et al. 1990). Other predator species additively influence nest predation on passerines in a variety of habitats (Savidge 1987, Suárez et al. 1993, Martin and Joron 2003), waterfowl (Sovada et al. 1995), and seabirds (Burger and Gochfeld 1994), supporting the Dominant Predator Hypothesis. Other studies conducted on tetranoids (Parker 1984), waterfowl (Greenwood 1986, Clark et al. 1995), and songbirds (Dion et al. 1999a), have found evidence of compensatory predation supporting the Nest Predator Diversity Hypothesis including. Nest predation abilities and ecology of the secondary nest predators relative to the primary predator are likely responsible for these differences among research findings (Fig. 2.1, Table 2.2). In Newfoundland, red squirrels are dominant nest predators because there are fewer potential nest predators to compensate than in other regions of North America (Dodds 1983). Songbirds also occur at lower densities than other regions of the boreal forest (Whitaker and Montevecchi 1997, Thompson et al. 1999), so it is likely energetically prohibitive for larger predators to search for nests. Finally, in many areas of Newfoundland, predators may find only ground nests accessible since moose remove much of the shrub layer (McLaren et al. in press).

The additive effects of red squirrels on nest predation are largely due to red squirrels depredating more ground nests relative to the native predators. This pattern is consistent with other studies in the boreal forest where red squirrels are among the primary predators but favour ground nests while Gray Jays depredate mostly tree nests (Darveau et al. 1997, Bayne and Hobson 1997). It is unclear whether this pattern is constant throughout the

Table 2.2. A framework with hypotheses, predictions, and mechanisms for predicting additive and compensatory hypotheses.

Hypothesis	Prediction	Mechanism
Dominant Predator Hypothesis	1) Removal of a primary predator will result in a commensurate decrease in nest predation[a] 2) Removal of both predators will result in minimal nest predation	1) no secondary predators 2) inefficient secondary predators 3) nests inaccessible to secondary predators
Nest Predator Diversity Hypothesis	Removal of one or both primary predators will cause little change in nest predation levels	1) efficient predators replaced by less efficient secondary predators 2) secondary predators freed from predation; meso-predator release 3) change in patterns of predation through nest access

[a] Decreases in nest depredation will be proportion to predation by removed predator species

boreal forest but it is likely in other areas with limited predator assemblages (Martin and Joron 2003). Red squirrels are unlikely to be a dominant nest predator in more predator rich, temperate forests (Reitsma et al. 1990), or in the western Canadian forests where other rodents are important nest predators (Bayne and Hobson 1997, Hannon and Cotteril 1998).

These findings suggest that before the introduction of red squirrels to Newfoundland, ground nesting songbirds experienced little predation pressure. Red squirrels may be changing patterns of nest predation and are possibly influencing nest site selection and other life history traits of forest songbirds. These patterns are likely to vary across Newfoundland owing to differences in the relative abundances of other predators, especially in continuous black spruce forests where Gray Jays are less common than in balsam fir forests (K. Lewis pers. obs.). However, it does not appear that red squirrels have greatly altered avian assemblages in Newfoundland. Although historical data on forest songbird abundance are limited, no avian species are known to have gone extinct since red squirrels were introduced, and Breeding Bird Surveys indicate that only the Tree Swallow (*Tachycineta bicolor*) has experienced a significant population decline (Sauer et al. 2003), although data are very sparse. In addition, Benkman (1993), suggested that red squirrels are responsible for the decline of the Newfoundland Red Crossbill (*Loxia percna percna*) through depredation of conifer cones. Squirrels could also similarly influence other cone-dependent finches (Wren and Montevecchi 2004). Based on the year red squirrels were introduced and observations by parks personnel, red squirrels could only have attained current densities in Gros Morne National Park and Terra Nova National Park since the mid-1980s and it is likely too early to predict their influence on forest songbirds at a landscape level.

2.5.2 PREDATOR MANIPULATION STUDIES

Existing studies suggest that variations in the influence of multiple predators on prey are likely to be determined by factors that promote intra-guild predation and behavioural interactions among predators such as overlap in predator foraging habitat and foraging characteristics, functional responses to prey density, habitat complexity (Sih et al. 1998), as well as food quality (Oedekoven and Joern 2000) and quantity (Anholt et al. 2000) for prey. Although logistically difficult and usually limited to fresh water organisms and terrestrial arthropods (Sih et al. 1998), a full factorial study design should be applied to nest predation studies. The findings from this literature should be used to generate hypotheses concerning interactions among nest predators and how they influence nesting birds.

Most predator manipulation studies investigating nest predation do not isolate the additive or compensatory effects of different nest predators *a priori*. Ultimately, predator manipulation studies should help to predict when additive or compensatory predation will occur based on the characteristics of the predator and prey assemblages. Additive nest predation will likely be common in systems with low predator richness (but see Parker 1984) and where the prey is naive, i.e. seabird colonies (Burger and Gochfeld 1994) and islands (Savidge 1987). If a top carnivore suppresses meso-predators, release from this predation through removal of the top carnivore can cause extreme compensatory predation (Rogers and Caro 1998). Predators, such as red squirrels, have access to virtually all nests in their respective ecosystems and experience energetic benefits from depredating nests, may be more likely to have additive effects. In summary, composition of the nest predator assemblage, the relative abilities of these predators, and interactions within this assemblage will likely determine whether a system demonstrates additive or compensatory nest predation with subsequent effects on nest-site selection, avian life history traits, and ecological patterns.

2.5.3 CONSERVATION AND THEORY

Except for the present work, few studies have explicitly tested the Dominant Predator/Nest Predator Diversity Hypotheses by removing or altering the behaviour of targeted nest predators (see Crabtree and Wolfe 1988, Reitsma et al. 1990, Martin and Joron 2003). Many studies have found post hoc evidence of additive or compensatory predation, yet the mechanisms that produce these patterns are rarely explored despite their importance for both conservation and general theories of nest predation.

The tremendous number of studies manipulating the predators of game birds and waterfowl (Newton 1998, Beauchamp et al. 1996) indicate the desire of managers to understand how controlling predator populations could influence avian populations (Greenwood and Sovoda 1996). Any management plan designed to increase nesting success must determine if removal of the primary nest predator(s) will decrease nest predation or simply create opportunities for other, less efficient predators (Dion et al. 1999a), especially if the species of interest is endangered (Sinclair et al. 1998). However, it is possible that at temporal scales longer than the breeding season, increased production due to predator removal is compensated for by other sources of mortality (Côté and Sutherland 1997). Despite great efforts to control nest predators, waterfowl managers have had mixed success in preventing general decreases in nesting success through predator manipulation (Beauchamp et al. 1996), and have only marginally increased nest success through habitat improvement (Garrettson and Rohwer 2001). Other methods may need to be employed to increase target populations such as increased food supply, creation of new habitat, or new nest sites, in addition to predator removal.

These hypotheses are also important for understanding patterns and processes underlying nest predation. Hypotheses concerning ecological patterns of nest predation lack generality. For example, hypotheses that habitat edges produce indirect biotic effects (i.e. edge effects) that influence nest predation have equivocal support (Patton 1994), have rarely been studied in a mechanistic fashion (Murica 1995), and do little to improve understanding of processes underlying nest predation (Donovan 1997). Similarly, nest concealment has differential effects on nest success (Filliater et al. 1994, Gotmark et al. 1995, Cresswell 1997). Understanding the functional role of different nest predators is an important step towards more general hypotheses of nest predation. Current understanding of such issues comes largely from small scale studies, while the game bird literature is focused primarily on additive/compensatory mortality, not the influence of individual predator species. I suggest, a preliminary, conceptual framework linking predator species richness and mechanisms that could lead to additive and compensatory predation (Table 2.2), leading to a greater understanding of how nest predation varies within and among habitats.

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Appendix 2.1. Nest predators on different nest types in black spruce and balsam fir forests in 2001 and 2002. EACH = Eastern Chipmunk, RESQ = red squirrel.

Year	Forest	Nest type	Treatment	EACH	Gray Jay	Red fox?	RESQ	RESQ?	Sciurid	Small mammal	Unidentified	Bird	Mammal
2001	Black spruce	Ground	Control				10				1		
			Treatment								1	2	
		Tree	Control		1		3	3					
			Treatment		1			1					
			Total		2		13	4			2	2	
2002	Balsam fir	Ground	Control		1		10	2		1			
			Treatment							1	1		
		Tree	Control		3		2		1			1	1
			Treatment	1	1								
			Total	1	5		12	2	1	2	1	1	1
	Black spruce	Ground	Control			2	10				1		
			Treatment					1					
		Tree	Control		3		6	1			4	2	
			Treatment				1	1			1	1	
			Total		3	2	17	3			6	3	

3.0 The influence of disturbance and herbivory on nest predation through their indirect effects on red squirrels.

3.1 ABSTRACT

I studied how patterns of nest predation may be indirectly influenced by succession, herbivores, and nest predator behaviour. Fire and defoliating insects create gaps in forested landscapes that are maintained on the island of Newfoundland by introduced moose (*Alces alces*) and snowshoe hare (*Lepus americana*) herbivory. After low-intensity burns, vegetation is dominated by *Kalmia angustifolia*, a shrub that is resistant to herbivory (high-cover gaps), whereas forbs and small woody shrubs dominate gaps created by defoliating insects (low-cover gaps). Differences in vegetative cover may influence the behaviour of the dominant nest predator, the introduced red squirrel (*Tamiasciurus hudsonicus*), indirectly influencing patterns of nest predation. To investigate these potential influences, I set out artificial nests along forest-gap edges in 2002 in eastern Newfoundland. Nests were placed 20 m from the edge in both forest and in gaps, in both insect and fire disturbed areas. Small mammal tracking stations were used to detect how quickly red squirrels use different habitat. Red squirrels visited tracking stations in forests significantly faster than in gaps and low-cover habitat (gaps and adjacent forests) significantly faster than in high-cover habitat. This pattern is likely due to coarse woody debris and increased food supply, reducing the risk and increasing the benefit of low-cover habitat. Differences in red squirrel habitat use may cause large differences in nest predation over the short avian breeding season. Nest predation was

significantly higher in forests than in gaps but other comparisons were not statistically significant. A framework for incorporating succession, herbivory, and nest predator behaviour into studies of nest predation is proposed.

3.2 INTRODUCTION

Nest predation plays an important role in structuring avian communities (Martin 1988a, 1988b, 1993, Wiens 1989). Communities are also structured by processes such as disturbance and successsion (Huston 1994), plant-herbivore interactions (Huntly 1991, Davidson 1993), plant-animal associations (Helle and Niemi 1996), predator-prey interactions (Lima and Dill 1990, Sih et al. 1998), and/or indirect effects (Wootton 1994). Nest predation is often studied independently of these other factors and processes, ignoring potential interactions that could influence patterns of nest predation (Fig. 3.1). For example, herbivores can dramatically influence successional pathways, plant composition, structure and production (Naiman 1988), especially when herbivore populations are maintained at artificially high levels (Frelich and Lorimer 1985, Alverson et al. 1988), the herbivore is an introduced species (Chapuis et al. 1994, McLaren et al. in press), or predators are absent (Crête et al. 2001). Successional sere, vegetative complexity and species composition, strongly influence avian composition (Cody 1985, Helle and Niemi 1996), foraging behaviour (Parrish 1995), and nest site selection (Martin and Roper 1988, Martin 1993). By modifying vegetation, herbivores may indirectly influence avian species composition (DeGraaf et al. 1991, Dobkin et al. 1998), and can also increase the probability of nest predation (Martin and Joron 2003, cf. Popotnik and Giuliano 2000) due to decreased amount of vegetation around nests (Martin 1993). Removal of vegetation by herbivores may also indirectly influence nest predators by affecting interactions with their own predators (Lima and Dill 1990). Dion et al. (1999,

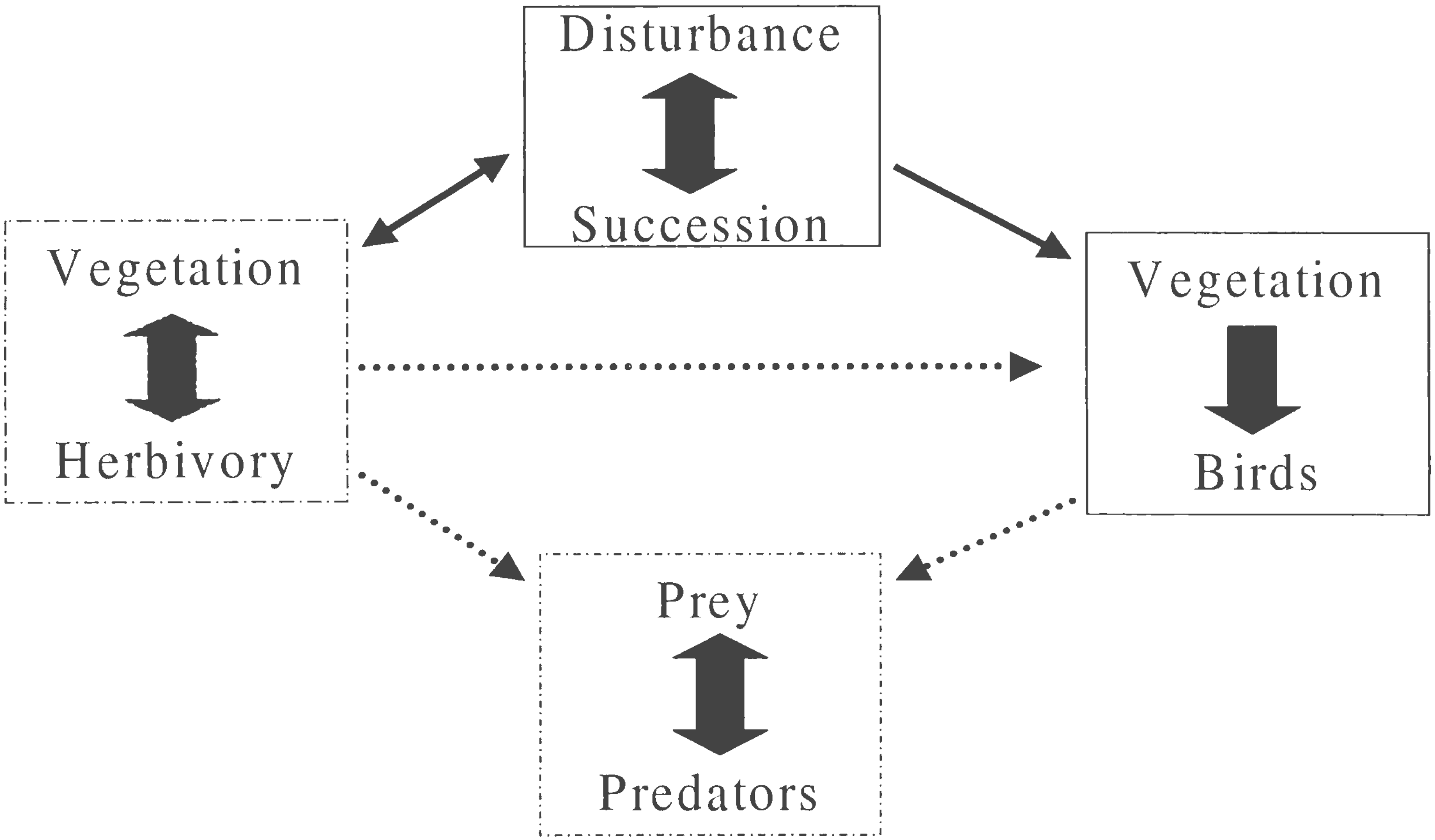

Fig. 1. Schematic framework of ecological studies. Boxes and block arrows indicate traditional areas of study with well studied interactions. Broken lines around the boxes indicate interactions that are not well understood in the context of avian ecology. Solid arrows between boxes indicate that interactions between boxes are well studied; dotted arrows between boxes indicate interactions between traditionally studied systems that could influence nest predation.

2000) showed that nest predators demonstrate a behavioural response to decreased vegetation height and density, presumably to avoid their own predators.

In this study, I explored how patterns of nest predation are indirectly influenced by interactions among herbivores, disturbance, and nest predator behaviour in the boreal forests of eastern Newfoundland, Canada. The introduction of moose (*Alces alces*), and potentially of snowshoe hare (*Lepus americanus*), have altered successional pathways and maintained gaps in forested landscapes (Thompson et al. 1992, Power 2000). Introduced red squirrels (*Tamiasciurus hudsonicus*) are the dominant nest predator in Newfoundland (Lewis 1999, Lewis and Montevecchi submitted), and common nest predators in boreal and coniferous forests (Vander-Haegan and DeGraff 1996, Darveau et al. 1997, Tewksbury et al. 1998). Like many rodents, red squirrels may avoid gaps and other open areas to minimize predation risk (Brown 1988, Guerra and Vickery 1998).

Specifically, I compared nest predation by red squirrels in forests and gaps, and explored how patterns of nest predation are indirectly influenced by interactions among herbivores, disturbance, and nest predator behaviour in eastern Newfoundland. In addition to more readily using forests than gaps, I hypothesize that red squirrels will more readily use gaps with greater vegetative cover due to decreased predation risk. I hypothesize further that if nest predation in Newfoundland is a function of red squirrel habitat use, then nest predation will be 1) higher in forests than in gaps, and 2) higher in gaps with high vegetative cover than gaps with low vegetative cover.

3.3 METHODS

3.3.1 STUDY AREA

Study sites were located in Terra Nova National Park (TNNP; 54° 00' W, 48° 30' N), in the Northcentral subregion of the Central Newfoundland ecoregion (Meades and Moores 1989) on the eastern coast of the island of Newfoundland, Canada. Black spruce (*Picea mariana*) is the dominant tree but balsam fir (*Abies balsamea*) are commonly found on more fertile soils. White birch (*Betula papyrifera*), trembling aspen (*Populus tremulodies*), alder (*Alnus* spp.) occur less frequently, whereas larch, (*Larix larcina*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) are rare throughout the park and this region. Peatlands, wetlands, and heathlands are common (Power 2000). Kalmia (*Kalmia angustifolia*), an ericaceous dwarf shrub, forms a thick, vigorous forest understory and is usually associated with open canopy black spruce forest and heathlands. A variety of disturbance types, combined with the variable hydrogeology, contribute to highly varied and fragmented habitat (Power 2000).

Fire, insects, wind, and a number of introduced herbivores, including moose, snowshoe hare, and red squirrels all influence forest vegetation and diversity. Low intensity fires resulting from fire suppression promote the spread of kalmia (Bloom 2001) which grows to the height of approximately one meter and is unpalatable to most herbivores (Thomson and Mallik 1989). As a result, kalmia dominates the vegetation (~ 1 m in height) in post-fire gaps (hereafter high-cover gaps), creating heathlands that can persist for decades or longer in Newfoundland (Meades 1983). The 29 heathlands in

TNNP comprise about 3 % of land area (average in TNNP = 12.9 ha), and in eastern Newfoundland, range in size from 0.04 ha to more than 23 000 ha (Power 2000,). In addition to kalmia, islands of surviving trees are common, and the surrounding forest is usually extensive and predominately black spruce.

Insect disturbance creates a very different landscape than fire. Balsam fir stands in Newfoundland are subject to periodic defoliation by insects (spruce budworm *Choristoneura fumiferana* and hemlock looper *Lambdina fiscellaria*) that kill the trees and create gaps in the remaining forest (Power 2000). There are about 293 of these gaps comprising approximately 3.5 % of TNNP, and they are much smaller than high-cover gaps, ranging in size from 0.01 to 82 ha (average = 4.8 ha, T. Harvey, pers. comm..). Forest regeneration in insect-kill gaps is often suppressed by moose and possibly snowshoe hare (Thompson and Mallik 1989, Power 2000). The resulting vegetation density and height is considerably lower in these gaps (hereafter low-cover gaps), consisting mainly of forbs, short grasses, some short kalmia (< 20 cm), and after the avian breeding season, ferns. Black spruce seems to be slowly invading these areas but is not a factor in this study (L. Hermanutz, pers. comm.). Gap configuration varied greatly depending on the composition of the former balsam fir stands. Prior to the insect kill, these balsam fir stands existed within a matrix of black spruce, black spruce scrub, and peatland. Consequently, the forests surrounding low-cover gaps are less extensive than in high-cover gaps. A few black spruce, birch, alders, balsam fir, and snags remain in low-cover gaps as well as large amounts of coarse woody debris. For consistency, I apply the terms high- and low-cover to the forests around the different gap types, although vegetation structure in the forests is more variable than in the gaps. For simplicity, when referring to the gaps and adjacent forests in one disturbance type collectively, I use the term high- or low-cover habitat.

3.3.2 NEST PREDATORS

Potential avian nest predators in Newfoundland include Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and Gray Jay (*Perisoreus canadensis*). Only Gray Jays and Ravens were observed on these study sites (Whitaker and Montevecchi 1997, K. Lewis pers. obs.). Both are uncommon, and Common Ravens were usually only seen flying over the study sites; only once did I observe a Common Raven in the forest, apparently foraging on the forest floor. Potential native mammalian nest predators include black bear *(Ursus americanus*), red fox (*Vulpes vulpes*), American marten (*Martes americanus*), short-tailed weasel (*Mustela erminea)*, and meadow vole (*Microtus pennsylvanicus*). Other introduced mammalian predators include red squirrel, mink (*Martes vison*), deer mouse (*Peromyscus maniculatus*), eastern chipmunk (*Tamias striatus*), boreal redback vole (*Clethrionomys gapperi*), and possibly masked shrew (*Sorex cineurus*; Dodds 1983). Deer mice are found regularly in western Newfoundland, (D. Snow and S. Gerrow pers. comm.), but are not a factor in eastern Newfoundland (J. Gosse pers. comm.). Eastern chipmunks are slowly spreading north in western Newfoundland and are found as far north as Gros Morne National Park (K.

Lewis, pers. obs.). Boreal red-back vole was probably introduced to western Newfoundland in 2000, but has not reached the eastern part of the island (J. Gosse pers. comm.).

Many nest predators in my study have been found in other boreal studies, but these other studies often have a far more diverse nest predator assemblages including other species of chipmunks, mice, mustelids, Black-billed Magpie (*Pica pica*), and striped skunk (*Mephitus mephitus*; Bayne and Hobson 1997, Boulet et al. 2000, Rangen et al. 2000). The potential predator assemblage is markedly reduced in Newfoundland, and many potential nest predators common to other parts of North America are absent including raccoon (*Procyon lotor*), striped skunk, gray squirrel *(Sciurus carolinensis)*, wood rats (*Neotoma* spp.), opossums, (*Didelphis virginiana*), gray fox (*Urocyon cinereorgenteus*), badgers (*Taxidea taxus*), many small rodents, and snakes.

3.3.3 STUDY DESIGN

A pilot study conducted in this area encountered several difficulties that influenced the subsequent study design. First, the habitat of eastern Newfoundland is extremely heterogeneous with highly variable habitat configurations and edges, varying densities of kalmia, alder, fire islands, and stands of trees that survived insect defoliation making it difficult to account for all of these secondary variables. In addition, small stands of forest adjacent to insect kills may contain few predators, contributing to very low predation rates (K. Lewis, unpublished data).

Using aerial photographs, I located gaps created by insect defoliation and fires within TNNP that were bordered by intact forest. Bordering forests were usually black spruce but occasionally balsam fir. I chose five low-cover gaps that varied in size but tended to be small (2-24 ha), although one site was part of a very large insect kill (82 ha). The two high-cover gaps were 332 ha and 201 ha respectively. Gaps were selected that were large enough to accommodate the study design, had relatively straight edges with large stands of bordering forest, and were accessible. Gaps were separated by several kilometers to ensure independence. At 50 m intervals along the gap edge, I established stations 20 m from the edge into the gap and the forest (Fig. 3.2). Within a gap, groups of stations were often separated by considerably more than 50 m, depending on edge suitability. There were five to 32 pairs of stations per gap depending on gap size and the suitability of the edge. The distance of 20 m from the edge was chosen because the objective of this study was to test how differences in vegetation, modified by herbivory, influence rodent foraging decisions and subsequently nest predation. This experiment was not designed to test for differences between disturbed and undisturbed habitat. Rodents have been shown to decrease foraging times when a food source is only 2-3 meters from protective cover (Brown et al. 1992, Guerra and Vickery 1998). Furthermore, the edges were quite distinct in these areas and the vegetation differed greatly on either side of the edge, even over 20 m. A larger distance would not test the question of the study and result in confounds with the secondary variables previously mentioned. The percentage of ground covered by kalmia and forbs at each station was estimated on a rank scale using the

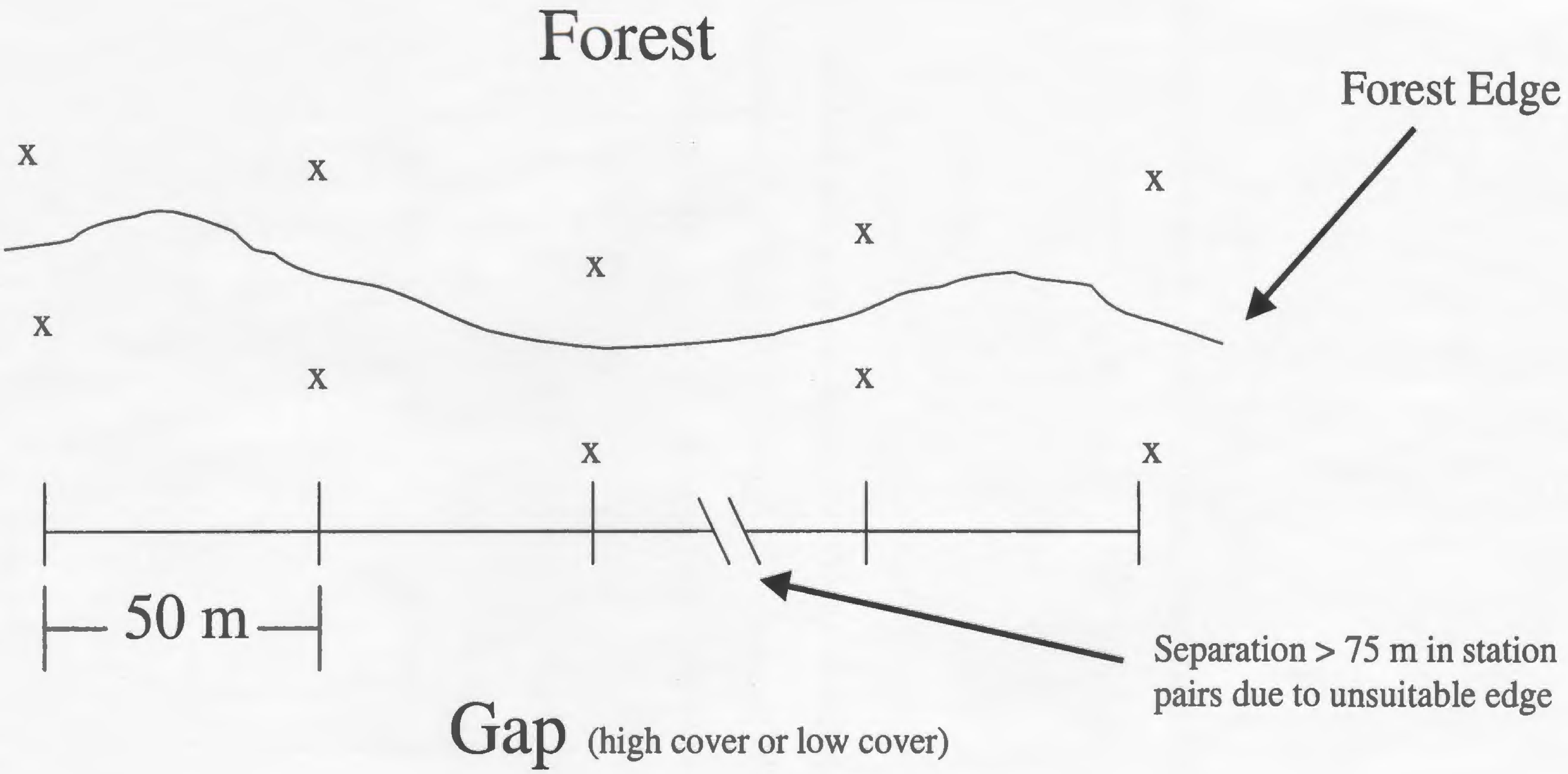

Fig. 3.2. A schematic overview of the study design, x = artificial nests. ~ 50 nests per gap type with an equal number in the forest. Tracking stations at every other station.

Braun-Blanquet method in a 4 m^2 plot (Barbour et al. 1980) in order to compare high- and low-cover habitat.

3.3.4 RED SQUIRREL HABITAT USE

To assess how readily red squirrels use different disturbance and habitat types, I used enclosed track plates (hereafter tracking stations, see Zielinski 1995 for a description). Pieces of sheet metal (~ 15 x 10 cm), coated with soot, and a piece of tacky, white paper of roughly the same dimension, were placed inside a 30 cm section of 7.68 cm (3") diameter PVC pipe. The soot adhered to an animal's foot as it entered the tracking station, and was transferred to the tacky side of the white paper at the rear of the tracking station. The back half of the tracking station was covered with duct tape to help waterproof the station. To minimize movement, tracking stations were weighted with coarse woody debris and staked into place with branches. I placed tracking stations with the end containing the white paper against a tree or rock at every other station from July 24-29. Tracks were identified using field guides. Tracking stations were baited with a mixture of rolled oats and peanut butter and checked every other day for a week. Previous tracking attempts in early June using sunflower seeds did not attract red squirrels even after several weeks. However, I do not expect this delay to change red squirrel habitat use or abundance since very few juveniles are present at this time (K. Lewis unpublish data).

3.3.5 NEST PREDATION

Natural bird nests are extremely difficult to locate in Newfoundland forests due to low density and difficult searching conditions. Therefore, similar to other studies of nest predation in the boreal forest (e.g. Darveau et al. 1997, Bayne and Hobson 1997), I used artificial nests. Despite the debate over their use, artificial nests may yield an index of actual nest predation (e.g. Wilson et al. 1998, Pärt and Wretenberg 2002), and nest predation has been shown to be similar between artificial and real nests in simple systems where red squirrels are the dominant predator (Martin and Joron 2003). Furthermore, artificial nests permit the investigation of mechanisms underlying nest predation in controlled experiments with adequate sample sizes (Schmidt et al. 2001).

Artificial nests (warbler-sized nest: 9 cm diameter x 3 cm depth) were baited with a Japanese Quail (*Coturnix japonica*) egg, an appropriate sized egg for the nest predator assemblage in Newfoundland (Lewis and Montevecchi 1999). To identify predators, a clay egg, imbedded with soil from the forest organic layer so that it approximated the appearance of the Japanese Quail egg, was attached to the nest with steel snare wire. Nests were lined with grasses and placed on the ground in extremely concealed locations that closely approximated the nest sites of Hermit Thrush (*Catharus guttatus*), Dark-eyed Junco (*Junco hyemalis*), and White-throated Sparrow (*Zonotrichia albicollis,* K. Lewis, pers. obs.); birds that are ubiquitous in forests and gaps in eastern Newfoundland (Lewis et al. 2000). Care was taken to insure that the wire was covered and would not attract predators. Nests were later relocated using flags and field notes of natural features. Nests were placed more than 5 m from the flags to reduce the likelihood of attracting predators to the nests. In an attempt to minimize human scent on artificial nests, Japanese Quail eggs were washed in water and air dried, nest baskets were aired out for at least two weeks prior to the experiment, and latex gloves were worn at all times when handling artificial nests . Scent trails, a problem with all nest studies, can also bias nest predation and is difficult to mask (Whelan et al. 1994, Donalty and Henke 2001, but see Skagen et al. 1999). To minimize scent trails, artificial nests were set out at all stations between June 11-14, 2002, and checked only once, two weeks later. A nest was considered depredated if any egg was missing or marked by a predator.

3.3.6 STATISTICAL ANALYSIS

Analyses of vegetative cover using the Braun-Blanquet method were performed using ANOVA (Neter et al. 1990) with DataDesk (Data Description Inc. 1996) and are reported as the rank ± standard deviation. I examined residuals for normality and constant variance. Red squirrel use of the different disturbance and habitat types was assessed using survival analysis with PROC LIFEREG (SAS Institute Inc. 1996), weighting the number of days that tracking stations went without being visited . Nest predation was analyzed using logistic regression, a special case of the generalized linear model appropriate for analyzing binary data (Agresti 1996, Lewis 2004) using PROC GENMOD (SAS Institute Inc. 1996). Differences in deviance among model terms are reported as ΔG with the degrees of freedom in the subscript. I used a Bonferoni adjustment on $\alpha =$

0.05 when performing post-hoc analyses. All results are reported as Type III analysis (analagous to adjusted sums of squares).

3.4 RESULTS

3.4.1 VEGETATION ANALYSIS

The percent of kalmia and forb cover around nests greatly differed between habitat and disturbance types (kalmia, $F_{1,190} = 26.9$, $P < 0.001$; forb, $F_{1,189} = 18.6$, $P = < 0.001$). Kalmia cover was greater in high-cover gaps (4.9 ± 1.5 on the Braun-Blanquet scale and hereafter) than in all other habitat types (high-cover forest 3.3 ± 1.4, low-cover forest 3.4 ± 1.9, low-cover gap 2.5 ± 1.8, all comparisons $P < 0.001$, Bonferoni adjustment for multiple comparisons applied) while forb cover was greater in low-cover gaps 5.0 ± 1.4) than in all other habitat types (high-cover forest 2.5 ± 1.3, low-cover forest 3.0 ± 1.4, high-cover gap 2.9 ± 1.4, all comparisons $P < 0.001$, Bonferoni adjustment for multiple comparisons applied). Differences in amount of kalmia and forb cover were not significantly different for all other comparisons ($P > 0.01$).

3.4.2 EFFECTS OF HABIT AND DISTURBANCE ON RED SQUIRRELS

Red squirrels were detected at 35 of 100 tracking stations and were the most common animal detected. In addition to red squirrels, I detected masked shrews at seven tracking stations in all habitat types. A meadow vole may have been present at one station though tracks could not be conclusively identified. Based on teeth marks in the PVC pipe, bears were present at several tracking stations.

The interaction between disturbance and habitat did not influence the time it took for red squirrels to visit the tracking stations ($\Delta G_1 = 0.04$, $p = 0.9$). However, tracking stations were visited significantly faster by red squirrels in forests than in gaps ($\Delta G_1 = 5.6$, $p = 0.02$), and in low compared to high cover habitat ($\Delta G_1 = 29.3$, $p < 0.0001$; Tables 3.1). Using a planned post hoc test, tracking stations were visited significantly faster by red squirrels in low-cover gaps than high-cover gaps (i.e. insect vs kalmia gaps; $\Delta G_1 = 14.6$, $p < 0.0001$).

3.4.3 EFFECTS OF HABITAT AND DISTURBANCE ON NEST PREDATION

Nest predation was very low in this experiment with less than 11 % of all nests being depredated (Table 3.1). The interaction between disturbance type and habitat was not significant ($\Delta G_1 = 2.9$, $P = 0.09$). Nest predation was significantly higher in forests compared to gaps (Table 3.1, $\Delta G_1 = 7.8$, $P < 0.01$). There was, however, not a significant difference in nest predation between high-cover and low-cover habitat ($\Delta G_1 = 0.7$, $P = 0.41$) nor between low-cover gaps and high-cover gaps ($\Delta G_1 = 2.1$, $P = 0.15$; Table 3.1). Of the 21 nests that were depredated, red squirrels depredated nine nests. Red squirrels

Table 3.1. The influence of the type of cover and location on the cumulative proportion of tracking stations visited by red squirrels and the proportion of depredated artificial nests.

		Tracking Stations Visit			Nest Predation	
Cover	Location	1	2	3	Proportion	Ratio
high	forest	3/19	5/25	6/25	10/50	0.2
high	gap	0/19	4/25	3/25	1/50	0.02
low	forest	13/25	13/25	13/25	6/45	0.13
low	gap	8/25	11/25	13/25	4/49	0.08

depredated seven nests in high-cover forests compared to one in high-cover gaps and one in low-cover gaps. One nest was likely depredated by a bear and another by a meadow vole. Predators could not be positively identified at ten nests due to either missing nests or removal of all the eggs.

3.5 DISCUSSION

Nest predation can be indirectly influenced by interactions among disturbance, herbivory, and nest predator behaviour (Fig. 3.1). Fire and defoliating insects regularly disturb the boreal forest (McCullough et al. 1998). In Newfoundland, herbivores influence regenerating vegetation, helping to maintain high and low-cover gaps and contributing to the large differences in cover therein. Red squirrels respond to natural disturbance and herbivory in boreal habitats; they more readily use forests than gaps, and low-cover more than high-cover habitat. This influence of disturbance and herbivory on nest predator habitat use can indirectly influence nest predation. Correspondingly, nest predation was higher in forests than in gaps, but did not differ between gaps.

3.5.1 EFFECTS OF HABITAT AND DISTURBANCE ON RED SQUIRRELS

Red squirrels visited the tracking stations more quickly in forests than gaps (Table 3.1). This is not surprising since red squirrels are forest specialists (Obbard 1987, Steele 1998), although it seems clear that the areas near the edges of low-cover gaps are clearly not inhospitable for red squirrels. However, predation risk strongly influences foraging decisions and habitat use in many species (Lima and Dill 1990), including red squirrels (Guerra and Vickery 1998), and is likely to increase with distance. Red squirrels were rarely seen more than 30 m into a gap. Therefore, I suggest that red squirrels use gap habitat less often, and enter gaps at a lower frequency, than adjacent forests.

Unexpectedly, red squirrels presence was consistently higher in low-cover than high-cover habitat. The richer soils and more broken canopy of low-cover forests (Power 2000, K. Lewis pers. obs) likely increase primary productivity resulting in increased cone production, positively influencing red squirrel density through increased food supply (C. Smith 1968, Kemp and Keith 1970, cf. Rusch and Reeder 1978). In addition, the generally fragmented nature of low-cover forests results in low core habitat area (Laurance and Yensen 1991), and hence, more red squirrels are in contact with edge habitat.

I also rejected the hypothesis that greater protection from predators for red squirrels results in greater use of high-cover gaps than low-cover gaps (Tables 3.1). On the contrary, red squirrels more readily used low-cover gaps than high-cover gaps. Besides the factors cited above, red squirrels may use low-cover gaps more than high-cover gaps because the risks of utilizing a gap may be relatively small due to low predator diversity (Dodds 1983, Gosse 1998), and abundant cover (i.e. woody debris, scattered trees, alder, snags). Food was also plentiful in low-cover gaps where red squirrels regularly foraged for dewberries (*Rubus pubescens*, K. Lewis, pers. obs.); in contrast, the high-cover gaps were likely to be devoid of food for red squirrels due to the nutrient poor, acidic soils of kalmia heaths (K. Lewis pers. obs., Power 2000). Therefore, factors other than vegetation cover likely influenced predation risk and alternate food sources could have determined how red squirrels utilize non-forest habitat. Larger sample sizes, radio telemetry, and behavioural observations including direct measures of red squirrel foraging ecology among habitat types (Brown 1988) would help to clarify these matters.

3.5.2 EFFECTS OF HABITAT AND DISTURBANCE ON NEST PREDATION

The avian breeding season in Newfoundland is short (Montevecchi and Tuck 1987), and differences in habitat use by red squirrels may influence levels of nest predation. There was a significant difference in nest predation between forest and gaps (Table 3.1). Therefore, I accept the hypothesis that nest predation is higher in forests than in gaps due to red squirrel abundance. The short distance between stations and edge (20 m) likely influenced the result and it is highly probable that nest predation and red squirrel presence will decrease with increasing distance into the gap, providing greater support for these hypotheses. These results are consistent with other studies in the boreal forest suggesting that nest predation is lower in gaps than in forests (Bayne and Hobson 1997, Hannon and Cotteril 1998 cf. Thurber et al. 1994). Clearly, differences in how vegetation regenerates within gaps, the relative food supply, and the interactive effect of these factors on nest predators can indirectly influence patterns of nest predation.

I reject the hypothesis that nest predation was higher in gaps with greater cover and protection from predators for red squirrels. Nest predation was actually marginally higher in low-cover gaps compared to high-cover gaps (Table 3.1). However, patterns of nest predation were consistent with patterns of red squirrel habitat use, indicating that suppression of vegetation by herbivores may not be a major factor influencing nest predation in non-forested habitat when food is abundant and predation risk is low.

The paradox of marginally higher nest predation but significantly lower red squirrel presence in high-cover compared to low-cover habitat may have occurred for several reasons. Red squirrels may have spent more time in the high-cover forest searching for alternate food like eggs because of low food supply and and lower predation risk. Variations in nest detectability due to differences in shrub cover could have increased predation risk in high-cover habitats. Although I did not measure nest concealment directly, cover around the nests varied and kalmia provided more cover for nests than forbs. Consistent with other studies in Newfoundland and the eastern boreal forest, this study suggested that mammalian predators other than red squirrels are of minor importance (Darveau et al. 1997, Boulet et al. 2000, Lewis and Montevecchi submitted). It is possible that corvids and other predators may play a more important role in nest predation during the nestling phase, when more visual and auditory cues are present due to increased parental and nestling activity (Martin et al. 2000). My results are suggestive concerning the indirect influence of the interaction between habitat and disturbance on nest predation. Future studies will help clarify these relationships.

3.5.3 INDIRECT EFFECTS

This study sheds further light on the importance of understanding indirect effects in a phenomenon influenced by as many factors as nest predation. Indirect effects are pervasive in ecological systems (Strauss 19991, Holt and Lawton 1994, Wootton 1994), and herbivory has been shown to indirectly effect small mammals (Hayward et al. 1997), insects (Rambo and Faeth 1999), estuarine communities (Levin et al. 2002), and reptiles (North et al. 1994). Avian communities can be negatively influenced by grazing livestock (Dobkin et al. 1998, Bock and Bock 1999), or browsing ungulates (Dobkin et al. 2002, McShea and Rappole 1997). In Newfoundland, it appears that herbivores modify successional pathways following a disturbance and that this influences nest predators and subsequent predation.

Many factors influence nest predation, so generalizing these results will require a good understanding of the ecosystem of interest (see Fig. 3.1). Herbivores often exert a large influence on vegetation when they are not native (Chapuis et al. 1994), maintained at artificially high levels (Dobkin et al. 1998, Bock and Bock 1999), and/or lack predators (Crête et al. 2001). The presence or absence of these factors will partially determine to what degree herbivores alter successional pathways and how strongly they indirectly influence not only birds, but also foraging decisions that result from the interactions between nest predators and their own predators (Dion et al. 1999, Lewis and Montevecchi submitted).

3.5.4 SUMMARY

Nest predation plays an important role in structuring avian communities (Martin 1988b), and is itself influenced by many factors. Past attempts to explain nest predation at a landscape level (i.e. edge effects and habitat fragmentation) have produced equivocal results (Paton 1994, Andrén 1995, Bender et al. 1998). While this study was not designed to examine edge effects, it is clear that herbivores can exert a strong influence on vegetative structure, which could alter habitat for birds, as well as nest site selection and nest predator behaviour. Conducting controlled experiments on these large scale processes is difficult, but studies that carefully consider direct and indirect effects, and the interactions among ecosystem components that could influence nest predation may provide more insight into how nest predation structures avian communities (Fig. 3.1).

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4.0 Mechanisms underlying nest predation by introduced red squirrels (*Tamiasciurus hudsonicus*) in the Newfoundland boreal forest

4.1 ABSTRACT

Patterns of nest predation have commonly been explained by either the predator-density or nest-concealment hypotheses, although results have been equivocal. An alternative, foraging theory model predicts probability of encountering a nest, environmentally induced variations in food supply, and nest characteristics will alter the behaviour of predators and prey resulting in different rates of nest predation.

Relatively simple systems to test nest predation hypotheses are the balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) forests of eastern and western portions of the island of Newfoundland, where the introduced red squirrel (*Tamiasciurus hudsonicus*) has been identified as a dominant nest predator. In 2000-2002, I used artificial nests to test these hypotheses. I measured red squirrel densities, nest concealment, and manipulated passive nest defense with decoy birds, food supplies for red squirrels with supplemental sunflower seeds, and nest characteristics with large and small nests.

Red squirrels depredated more nests than any other identified predator and were found at higher densities in black spruce than in balsam fir forests in two of the three years. In general, nest predation increases slightly with red squirrel density, but differences between forest type could be more important. Nest concealment varied but

had little influence on nest predation. Passive nest defense had little influence on nest predation. The influence of supplemental food varied among years but was always greater in balsam fir forests. Larger nests were slightly more vulnerable to predation. In general, the support for the foraging theory model is not strong, but this may be typical of the boreal forest where nest predation is predicted to be largely incidental. However, I argue that this model is heuristically valuable for generating hypotheses about nest predation and that departures from model predictions are useful for understanding nest predation.

4.2 INTRODUCTION

Many hypotheses have been proposed to explain patterns of nest predation, but few studies explicitly examine nest predation as a complex predator - prey interaction (Schmidt 1999). Most studies presume a relationship between predators and the landscape (e.g. edge effects, habitat fragmentation, the nest predator density hypothesis, Wilcove 1985, Dijack and Thompson 2000, Chalfoun et al. 2002) and the influence of nest - site characteristics (e.g. nest concealment hypothesis, Martin 1993, Götmark et al. 1995). However, many studies lack direct tests of predator densities (Chalfoun et al. 2002), and the influence of nest concealment on nest predation is equivocal (Filiater et al. 1994, Cresswell 1997). This variation in results among studies may be due in part to variation in local predator assemblages (Miller and Knight 1993, Sieving and Willson 1998), environmental influences (Schmidt 1999, Ostfeld and Keesing 2000), a nest predator's behaviour within a landscape mosaic (Andrén 1995, Hartley and Hunter 1997), and predator-prey interactions (Schmidt 1999).

To better explain this variation in nest predation, Schmidt (1999) proposed an alternative to the traditional nest - predator - density and nest - concealment hypotheses with a model describing nest predation patterns based on foraging theory. Under the model, a predator actively searching for nests has a harvest rate influenced by the benefits of depredating a nest, and the costs of handling prey, an unsuccessful attack, and recognition of active and inactive nests. The model predicts that the harvest rate will be influenced by 1) search strategies and encounter probabilities, 2) nest defense and factors influencing nest vigilance, 3) alternate food supply and missed opportunity costs of foraging for the nest predator, and 4) habitat structure and nest-site characteristics.

While aspects of Schmidt's model have been investigated (Jones et al. 2002), the full model has not been rigorously tested. I simultaneously tested Schmidt's model and hypotheses relating nest predation levels to predator density and nest concealment in the boreal forests of Newfoundland using introduced red squirrels (*Tamiasciurus hudsonicus*) as the study subject. Previous research has shown that red squirrels are a dominant nest predator in Newfoundland (Lewis and Montevecchi submitted) and throughout much of their range (e.g. Vander-Haegan and DeGraff 1996, Darveau et al. 1997, Bayne and Hobson 1997, Tewksbury et al. 1998). Red squirrels were introduced to Newfoundland in the 1960s and have since spread to all forested areas of the island. Newfoundland presents several advantages for studying nest predation (Payne 1976). The island has fewer potential nest predators than other regions of the boreal forest (Bergerud 1983). Furthermore, the forests of Newfoundland can be broadly categorized into black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) dominated forests (Meades and Moores 1989), and red squirrel densities appear to be lower in fir forests (Wren 2001). Also, agriculture is rare, comprising less than 1% of the landmass, and geographically restricted in Newfoundland so studies are not confounded by species like corvids whose populations tend to increase with human development (Andrén 1992, also Bayne and Hobson 1997). Nest parasitism is not a concern because Brown-headed Cowbirds (*Molothrus ater*) are very uncommon (Mactavish et al. 2003).

Specifically, I tested the following hypotheses in an artificial nest experiment. First, the nest predator density hypothesis predicts that nest predation will increase with predator density. Second, the nest concealment hypothesis predicts that nest predation will decrease with increased amounts of vegetative cover due to decreases in visual, auditory, and olfactory cues for predators. Third, following Schmidt (1999), I also predict that nest predation will 1) be lower on nests "guarded" by decoy birds, i.e. passive defense, 2) decrease with the addition of supplemental food (sunflower seeds), and 3) be higher on large (thrush sized) nests than small (warbler sized) nests. I also generated two secondary hypotheses from Schmidt (1999). Klenner and Krebs (1991) suggest that food is a limiting factor controlling red squirrel densities. If this is true, depredating a nest will have a greater benefit for a red squirrel in poorer quality balsam fir forests compared to black spruce, and they should be more willing to incur the cost of attacking a "guarded" nest. Supplemental food should also be of greater benefit to red squirrels in balsam fir forests. I therefore predict that nest predation on guarded nests will be higher in balsam fir forests than black spruce, and that nest predation will decrease more in balsam fir forests than black spruce when supplemental food is provided.

4.2.1 Study Area

In order to provide comprehensive tests of the above hypotheses in Newfoundland, study sites were established in the two dominant forest types on the island of Newfoundland: black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Study sites in Terra Nova National Park (54° 00' W, 48° 30' N) in eastern Newfoundland were located in the North-central Subregion of the Central Newfoundland ecoregion (Meades and Moores 1989). This region is dominated by black spruce but balsam fir are commonly found on more fertile soils. White birch (*Betula papyrifera*), trembling aspen (*Populus tremulodies*), and alder (*Alnus* spp.) occur less commonly, whereas larch, (*Larix larcina*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) occur rarely throughout the park and this region. Peatlands, wetlands, and barrens are common (Power 2000). Sheep laurel (*Kalmia angustifolia*) is a dominant understory shrub, associated with black spruce forest and barrens. A diverse assemblage of vascular plants, moss, and lichens are found in this area. Fire, insects, wind, and a number of introduced herbivores, including moose (*Alces alces*), snowshoe hare (*Lagopus americanus*), and red squirrels, all influence the vegetation and diversity of these forests. Disturbance combined with the variable hydrogeology contribute to a highly varied and fragmented ecosystem (Power 2000).

Study sites in Gros Morne National Park (49° 40' W, 57° 45' N) were located in the Corner Brook Subregion of the Western Newfoundland Ecoregion, characterized by a rugged topography and generally nutrient rich soils (Meades and Moores 1989). Balsam fir and white birch are the dominate tree species, with lesser amounts of white spruce (*Picea glauca*) and black spruce. The latter is often found primarily on bedrock outcrops and poorly drained sites. Peatlands are less common than in Terra Nova National Park.

Ericaceous shrubs are rare and heaths develop only in very small areas. Disturbances are similar to Terra Nova National Park except that defoliation by insects such as hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) is the dominant disturbance type rather than fire (Meades and Moores 1989).

Study sites were selected in mature forest stands throughout both parks without a priori knowledge of squirrel density. I chose sites that were as similar as possible and avoided insect kills, bogs, roads, cut blocks, power line corridors, scrub spruce, and other edges although this was not always possible due to the highly variable, fragmented nature of these forests. The eight study sites in black spruce forests were located mostly in the northern part of Terra Nova National Park while the eight study sites in balsam fir forests in Gros Morne National Park were located mostly around Lomond River, Barter's Brook, and the town of Wiltondale. Ground cover in black spruce forests was dominated by moss. The understory was composed of patches of forbs and *Kalmia angustifolia* although on several sites, *K. angustifolia* dominated. Moss was not as prevalent in balsam fir forests; leaf litter was the common ground cover in some areas. The understory of balsam fir sites was composed largely of forbs.

4.2.2 Nest predators

Potential avian nest predators in Newfoundland include Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and Gray Jay (*Perisoreus canadensis*). During six years of field work in these areas, only Gray Jays and Common Ravens were observed on these study sites (K. Lewis pers. obs.), but both were uncommon. Common Ravens were usually seen flying over the study sites; only once was a Common Raven seen in the forest. Potential native mammalian nest predators include black bear *(Ursus americanus*), red fox (*Vulpes vulpes*), American marten (*Martes americanus*), short-tailed weasel (*Mustela erminea)*, and meadow vole (*Microtus pennsylvanicus*). Other introduced mammalian predators include red squirrel, mink (*Martes vison*), deer mouse (*Peromyscus maniculatus*), eastern chipmunk (*Tamias striatus*), boreal redback vole (*Clethrionomys gapperi*), and possibly masked shrew (*Sorex cineurus*, Dodds 1983). Deer mice occur in Gros Morne National Park and western Newfoundland (S. Gerrow and D. Snow pers. comm.), but do not yet occur in eastern Newfoundland (J. Gosse pers. comm.). Eastern chipmunks are slowly spreading north in western Newfoundland and are found as far north as Gros Morne National Park (K. Lewis pers. obs.). Boreal red-back vole was introduced to western Newfoundland circa 2000, but have not reached Terra Nova or Gros Morne National Parks (S. Gerrow and J. Gosse pers. comm.).

Many of the above nest predators have been found in other boreal studies, which usually have a far more diverse nest predator assemblages including other species of birds, chipmunks, mice, mustelids (e.g. striped skunk *Mephitus mephitus*, and Black-billed Magpie *Pica pica*, Bayne and Hobson 1997). Newfoundland lacks many potential nest predators common to other parts of North America including raccoon (*Procyon lotor*), striped skunk, gray squirrel *(Sciurus carolinensis*), wood rats (*Neotoma* spp.), opossums, (*Didelphis virginiana*), gray fox (*Urocyon cinereorgenteus*), badgers (*Taxidea taxus*), many small rodents, and snakes.

4.3 METHODS

4.3.1 RED SQUIRREL DEMOGRAPHY

A combination of mark-recapture based on trapping and sight records is probably the best way to estimate populations (Flyger 1959), but this approach was not feasible due to forest density and low numbers of red squirrel observations. Therefore, I estimated red squirrel densities on grids during the avian breeding season, with live-trapping methods (e.g. Klenner and Krebs 1991, Sullivan and Klenner 1993). I established trapping grids (240 x 240 m) with 25 evenly spaced trapping stations in both balsam fir and black spruce forests. Due to patches in the forest canopy, one grid in balsam fir forests had only 23 stations, and two grids in black spruce forests were 240 x 200 m. In each forest type, there were four trapping grids 2000/2001 and six in 2002. In 2000, there were two trapping sessions in May, but only one in balsam fir forests due to snow conditions and inclement weather that prevented trapping. There were two trapping sessions in July in both forest types. There was one trapping sessions in May and July on all grids in 2001 and 2002. Traps were set for two days in each trapping session, baited with peanut butter and an apple slice to prevent dehydration, opened at dawn, and checked 4-6 hr later. Traps were not open during inclement weather. Captured squirrels were ear tagged (using modified pliers, R. A. Lautenschlager) and weighed (± 5g) using a Pesola spring-balance scale. Sex and breeding condition were recorded, and age classes of the red squirrels were estimated by weight (Klenner and Krebs 1991). This protocol was approved by the Memorial University Animal Care Committee.

4.3.3 ARTIFICIAL NESTS

Artificial nests are commonly used to study nest predation, especially in the boreal forest (e.g. Darveau et al. 1997, Bayne and Hobson 1997). Despite the debate over their use, artificial nests may yield an index of actual nest predation (e.g. Wilson et al. 1998, Pärt and Wretenberg 2002), and nest predation has been shown to be similar between artificial and real nests in simple systems where red squirrels are the dominant predator (Martin and Joron 2003). Furthermore, artificial nests permit the investigation of mechanisms underlying nest predation in controlled experiments with adequate sample sizes (Schmidt et al. 2001a).

Artificial nest grids (25 evenly spaced nests at 60 m intervals) were established over trapping grids beginning on 5 June 2000, 8 June 2001, and 8 June 2002, and checked two weeks later. Squirrel trapping did not occur at this time. In addition to the trapping grids, I established two additional nest grids in 2000 (10 total grids), two in each forest type in 2001 (14 total grids), and two more in balsam fir forests in 2002 (16 total grids).

Artificial ground nests were placed in the most appropriate vegetative cover at each station. Nests were lined with grasses and placed on the ground in extremely concealed locations that closely approximated the locations of the Hermit Thrush (*Catharus guttatus*), Dark-eyed Junco (*Junco hyemalis*), and White-throated Sparrow (*Zonotrichia albicollis*) nests that I have found. Artificial nests were baited with a Japanese Quail (*Coturnix japonica*) egg, an appropriate sized egg for the nest predator assemblage in Newfoundland (Lewis and Montevecchi 1999). To identify predators, a clay egg, imbedded with soil from the forest organic layer so that it approximated the appearance of the Japanese Quail egg, was attached to the nest with carefully concealed, steel snare wire. Despite difficulties in determining predator identify with clay eggs (Marini and Mello 1998), I feel that this bias is minimal in Newfoundland due to low predator diversity. Nests were later relocated using flags and field notes of natural features. Nests were placed more than 5 m from the flags to reduce the likelihood of attracting predators to the nests. To minimize human scent, Japanese Quail eggs were washed in water and air dried, nest baskets were aired out for at least two weeks prior to the experiment, rubber gloves were worn at all times when handling any part of the nest apparatus, and rubber boots were worn when setting out the nests. Predators were identified by marks left in the clay eggs. In all years, concealment was measured by placing a box with 25 dots on each nest, and counting the number of dots that could be seen from a distance of 1 m directly over the nest. The fewer number of visible dots equates to greater concealment.

4.3.4 EXPERIMENTAL DESIGN TO TEST SCHMIDT'S MODEL

To test Schmidt's model (Schmidt 1999), I employed several different types of nests and randomly assigned them to each artificial nest site on all grids. The first nest type is the control nest (warbler-sized nest: 9 cm diameter x 3 cm depth, control nests hereafter). Second, to test for the influence of vigilance on nest predation, I placed a Styrofoam model of a bird resembling a Hermit Thrush (bird nests hereafter), a passerine that commonly nests on the ground (Ehrlich et al. 1988), next to the selected artificial nests. This form of passive defense has been shown to decrease nest predation by corvids (Martin 1992, cf. Schmidt 1999) and suggests that adults attending nests can be sufficient to prevent nest predation. Third, to test the influence of nest characteristics on nest predation, I used a larger nest type (thrush-sized nest: 13 cm diameter x 5 cm depth, large nests hereafter).

During 2000, to test the influence that alternate food sources have on nest predation patterns, I randomly allocated supplemental food to half of the grids in each forest type at the same time that the artificial nests were set out. In 2001, I reversed the supplemental food treatment among grids. In 2002, due to variable results and new grids, I again randomly allocated supplemental food to half the grids. The alternate food was meant to distract red squirrels from artificial nests, not cause a numerical response. Therefore, based on values from Klenner and Krebs (1991), Sullivan and Klenner (1993), and W. Klenner (pers. comm.), I placed approximately 4 kg/ ha of seed on each grid. Sunflower seeds were placed on the ground in small piles (e.g. Klenner and Krebs 1991, Sullivan and Klenner 1993) at 16 stations on the grid ~ 42 m from nest stations (Fig. 4.1), either

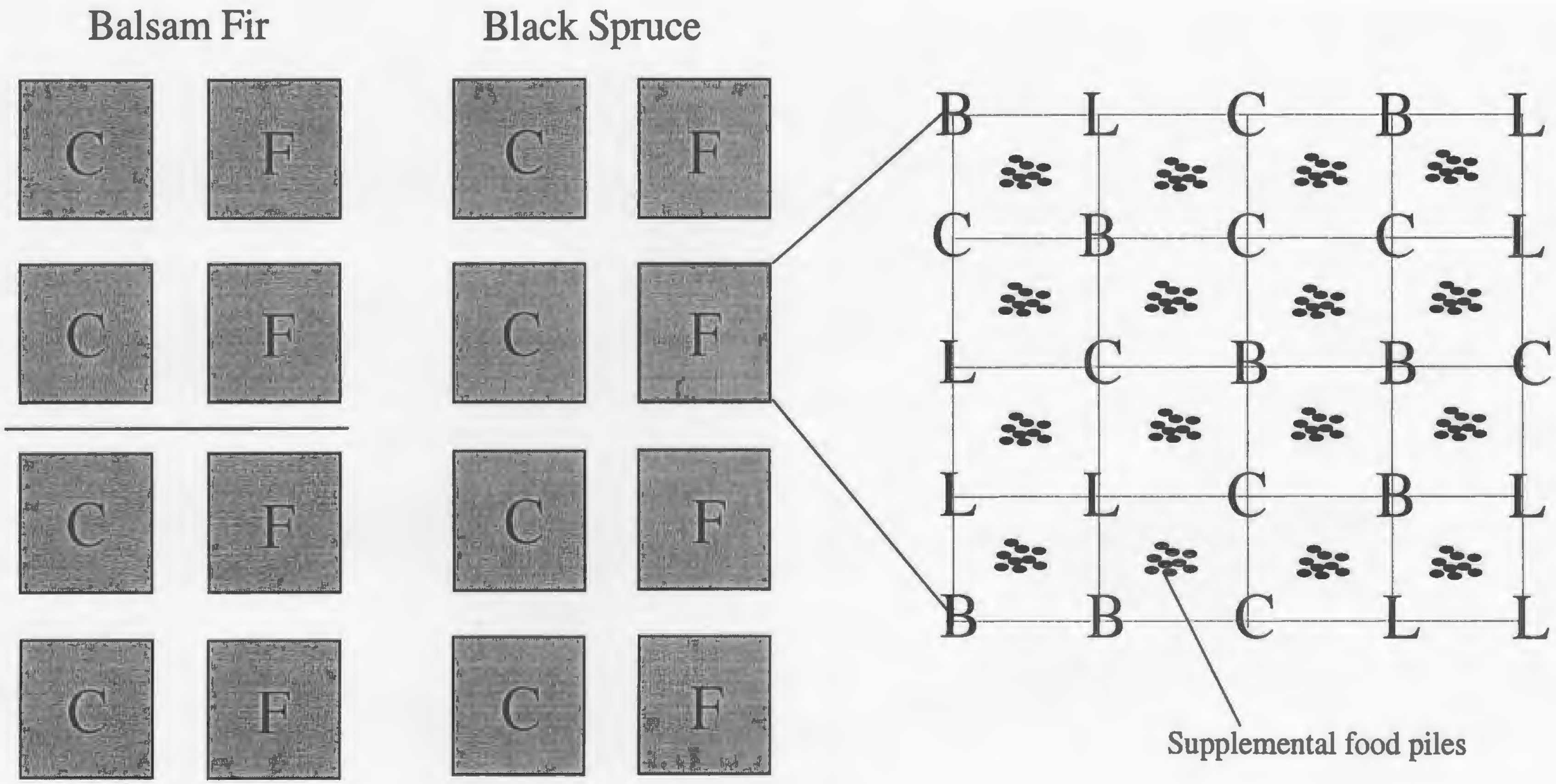

Figure. 4.1. Overview of the study design. Grids (240 m x 240 m) were either control (C) or food supplemental (F). On the right is an example of the randomly distributed nest types (Bird = B, Control = C, Large = L).

four days before nests were set out or on the same day. Black bears depredated the sunflower seed piles on two different grids in 2001 and 2002. One grid in 2002 was removed from the analyses because it was trap-lined by black bears and all nests were depredated.

4.3.5 STATISTICAL ANALYSIS

I estimated population sizes for adult red squirrels on each grid using the robust design model with the Huggins population estimate (Pollock 1982, Kendall 2001). Juvenile red squirrels were eliminated from these analyses since they were only trapped in late July, and unlikely to be a factor in nest predation in June. The robust design model combines traditional Jolly-Seber models that are normally employed to estimate red squirrel populations (e.g. Klenner and Krebs 1991) with closed population models (Kendall 2001). The robust design model takes advantage of multiple trap occasions (secondary sampling period) within a trap session (i.e. primary sampling period) to obtain less biased and more efficient estimates of survival, capture, recapture, and population size. Jolly-Seber models often give estimates for survival that are robust to heterogeneity in detection but its abundance estimator does not (Kendal 2001). All analyses were performed in program Mark (White and Burnham 1999). I included a covariate for tag loss in these models although it made little difference in the final estimates. Population estimates were then averaged between May and July for subsequent analyses.

To test for the differences in red squirrel density between forest types and years I used

ANOVA. Planned comparisons between black spruce and balsam fir forests for each year were conducted using a one tailed t-test, using a Bonferroni adjustment on $\alpha = 0.05$. When other comparisons suggested themselves, I conducted a least significant difference post-hoc comparison. I also tested to see if red squirrel density within forests differed among grids using a randomized block design, analogous in this case, to a paired comparison (Zar 1999) where year was the explanatory variable and grids were the blocking variable. Differences in nest concealment due to forest type, food supplementation, and nest type were tested for each year using three-way ANOVA. Analyses were conducted on Data Desk (Data Descriptions Inc 1996). On all tests, I examined residuals for normality and constant variance.

Differences in predation on artificial nests were tested using logistic regression, a special form of the generalized linear model used for the analysis of binary or proportional response variables with multiple explanatory variables (Agresti 1996), as is most appropriate for these data (Lewis 2004). Analyses were performed using PROC GENMOD (SAS Institue 1989-96). Differences in deviance among model terms are reported as ΔG with the degrees of freedom as a subscript. The influence of red squirrel density and forest type on nest predation were analyzed using an approach analogous to ANCOVA. Therefore, I first tested for interaction terms, and discarded them from the model when these were not significant. Data were divided and analysed as separate regressions if the interaction term was significant (Sokal and Rohlf 1995, Littell et al. 2002). I also tested the influence of nest concealment on nest predation. Using all the grids, the influence of nest, grid, and forest type on nest predation were used to test Schmidt's (1999) model and in the other analyses. All results are reported as Type III analysis (analogous to adjusted sums of squares). I used the CONTRAST statement in PROC GENMOD to perform planned comparisons among nest types (Littell et al. 2002).

4.4 RESULTS

4.4.1 PREDATORS

In all years, red squirrels depredated many more nests than any other predator (Appendix 4.1). There were also many nests where the predator could not be identified due to the absence of both eggs or the entire nest. Bears, birds, mustelids, and other small mammals depredated a few nests but were not a major factor in this study (Appendix 4.1).

4.4.2 RED SQUIRREL DENSITY

Consistent with predictions, average adult red squirrel densities were 2.24 and 1.62 times greater in black spruce than balsam fir forests in 2000 and 2001 (Fig. 4.2, Appendix 4.2). However, in 2002, red squirrel density was 1.23 times higher in balsam fir forests than in black spruce forests due to a dramatic decline in average red squirrel densities in black spruce forests (Fig. 4.2, Appendix 4.2). As a result, the interaction between forest and year significantly influenced red squirrel density ($F_{2,22} = 4.308$, $p = 0.0264$). Differences in red squirrel densities between forests was significantly different in 2000 (

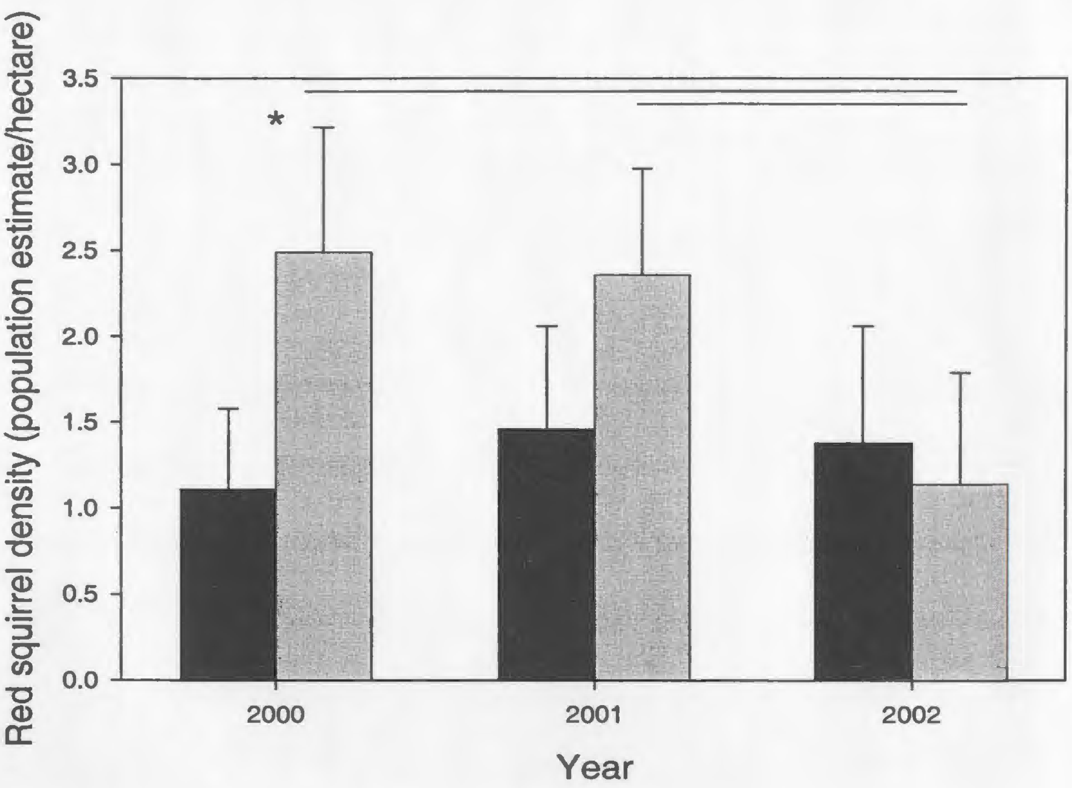

Figure 4.2. Mean red squirrel density (±SD) in balsam fir (black) and black spruce (gray) forests in Newfoundland from 2000-02. * indicates within year differences between forests. Lines indicate differences between forests among years.

$t_5 = 3.167$, $p = 0.0120$), nearly so in 2001($t_5 = 2.103$, $p = 0.0401$, and not significant in 2002 ($t_9 = 0.6259$, $p = 0.7273$, Bonferroni adjustment for multiple comparisons ($\alpha = 0.0167$) applied to all tests) Fig. 4.2, Appendix 4.2). I consider the differences in red squirrel densities in 2001 to be biologically significant given the effect size and the small sample size.

Average adult densities did not differ among years in balsam fir forests ($F_{2,5} = 0.6489$, $p = 0.5616$), but did in black spruce forests ($F_{2,6} = 5.7231$, $p = 0.0407$) with both 2000 and 2001 having significantly greater red squirrel densities than 2002 (2000 v 2002: $t_6 = 2.986$, $p = 0.0243$; 2001 v 2002: $t_6 = 3.001$, $p = 0.0204$, Bonferroni adjustment for multiple comparisons applied, $\alpha = 0.025$). There was no difference in red squirrel density between control and food supplemental grids in any year (2000: $t_5 = 0.706$, $p = 0.7457$; 2001 $t_4 = 0.7586$, $p = 0.2438$; 2002: $t_5 = 1.699$, $p = 0.9265$). Red squirrel density did not differ between May and July in 2000 and 2002 (2000: $t_7 = 1.281$, $p = 0.2409$; $t_{11} = 1.427$, $p = 0.1813$), but density was significantly lower in July than in May in 2001 ($t_7 = 4.198 = 0.0040$).

4.4.3 DENSITY AND NEST PREDATION

In general, nest predation moderately increased with red squirrel density (Figs. 4.3, 4.4). In 2000, the interaction term was not significant ($\Delta G_1 = 0.05$, $p = 0.8188$), and nest predation significantly increased with red squirrel density ($\Delta G_1 = 7.30$, $p = 0.0069$) and differed between forest type ($\Delta G_1 = 4.68$, $p = 0.0305$). The interaction between

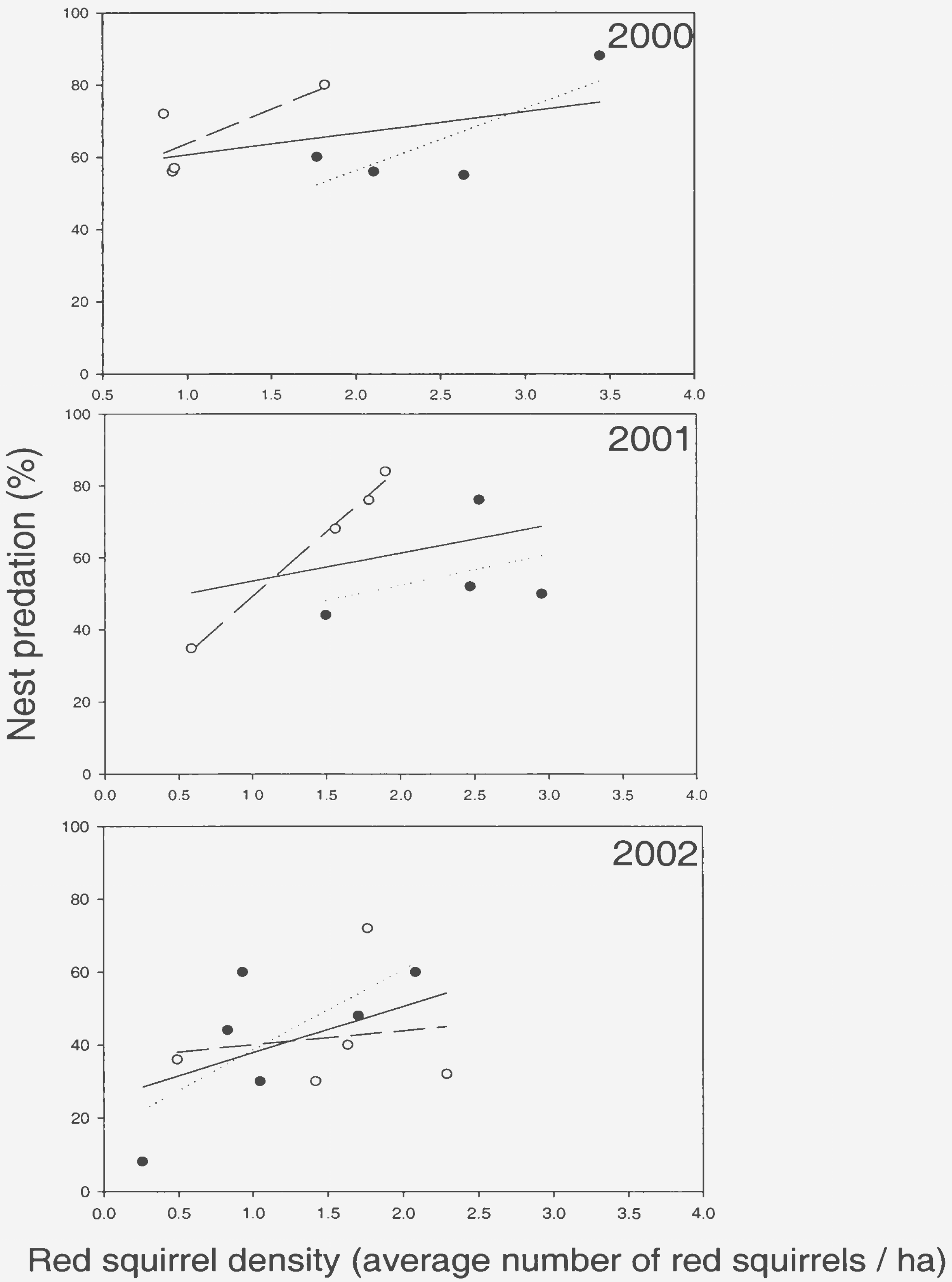

Figure 4.3. The influence of red squirrel density on nest predation in balsam fir (open circles - dashed lines), black spruce (closed circles - dotted lines), and both forests (solid lines) from 2000 - 2002.

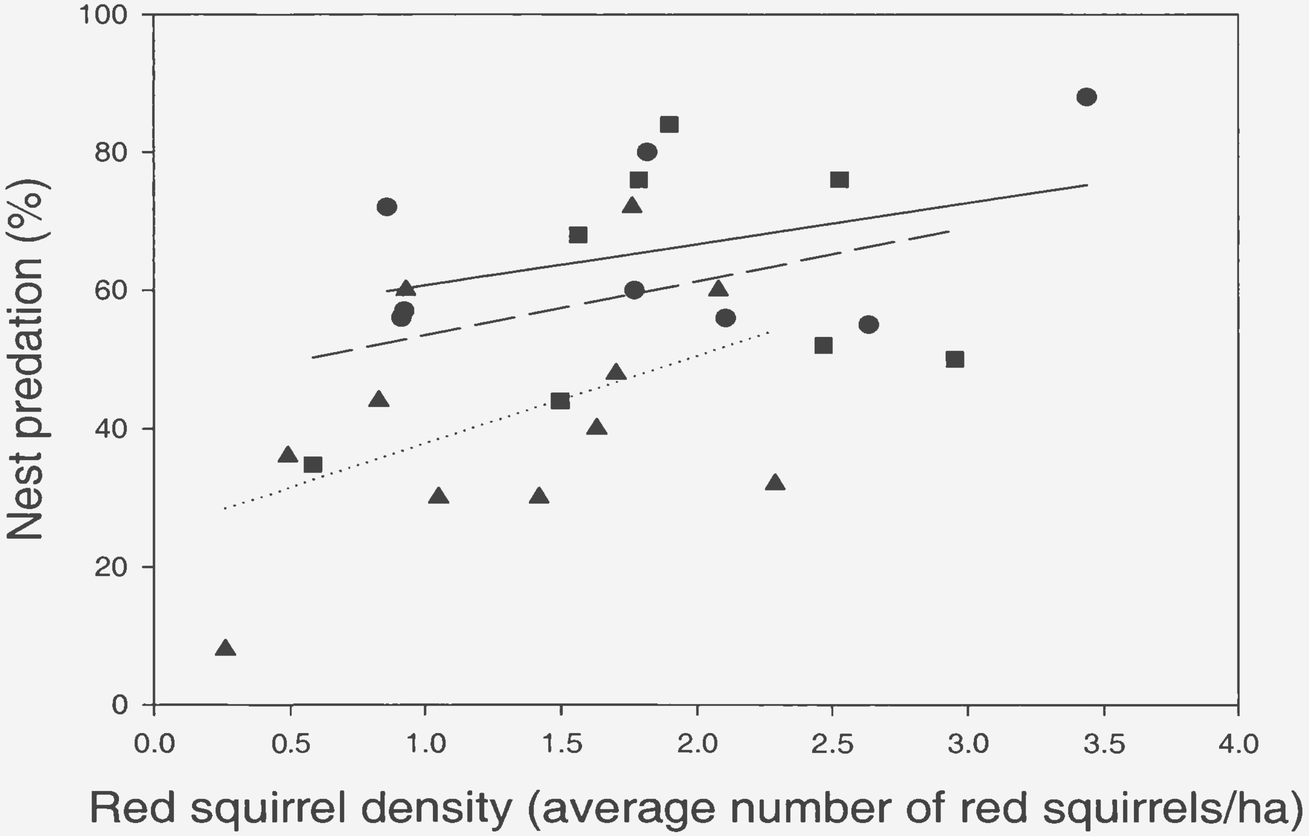

Figure 4.4. The influence of red squirrel density on nest predation for 2000-2002. The solid line is the regression line from 2000 (circles), the dashed line for 2001 (squares), and dotted line for 2002 (triangles).

forest and density was significant in 2001 ($\Delta G_1 = 4.16$, $p = 0.0413$), and nearly so in 2002 ($\Delta G_1 = 3.58$, $p = 0.0585$, 4.3, 4.4). When I divided the analyses between forest types, density significantly and positively influenced nest predation in balsam fir in 2001 ($\Delta G_1 = 14.28$, $p = 0.0002$) and black spruce in 2002 ($\Delta G_1 = 11.23$, $p = 0.0008$).

4.4.4 NEST CONCEALMENT AND ITS INFLUENCE ON NEST PREDATION

Nests were more concealed in black spruce forests than in balsam fir in all years, although differences were small ($p < .02$ in all years, Appendix 4.3). Differences in concealment were small between food supplemental grids, and among nest types (Appendix 4.3). Despite these differences, nest concealment did not influence nest predation (balsam fir 2000 - 2001, black spruce 2000 -2002: $p > 0.20$), except in balsam fir forests in 2002 ($\Delta G_1 = 7.76$ $p = 0.0054$).

4.4.5 SCHMIDT'S MODEL

In 2000, forest type did not influence nest predation, which was higher on control grids than food supplemental grids as predicted (Table 4.1, Fig. 4.5, Appendix 4.4). Large nests were depredated more often than control nests and the difference was nearly significant (Table 4.1). Nest predation was much higher in balsam fir forests than black spruce, and on food supplemental compared to control grids in 2001, when there was no difference in predation on nest types. Nest predation was not influenced by forest type in 2002. Although differences were not statistically significant, large nests were depredated more than control nests and food supplemental grids more than control grids (Table 4.1,

Table 4.1. Analysis of Deviance tables of the logistic regression models analyzing the influence of forest type, grid treatment and nest treatment on nest predation. The change in deviance between model terms is denoted by ΔG. The number of grids are in parentheses by year. The planned comparisons of nest type comparing the influence of passive nest defense and nest size are also presented. The number of grids are in parentheses.

Year	df	2000 (8)		2001 (14)		2002 (15)	
Source		ΔG	P	ΔG	P	ΔG	P
Forest Type	1	2.62	0.1052	13.59	0	0.1	0.7126
Grid Treatment	1	7.45	0.01	22.57	<0.0001	2.9	0.091
Nest type	2	3.45	0.1783	5.05	0.08	0.1	0.7389
Forest x Grid	1	0.81	0.3672	1.04	0.3072	3.3	0.1941
Forest x Nest	2	0.13	0.9391	3.44	0.1793	0.4	0.8165
Grid x Nest	2	3.37	0.1853	0.7	0.7048	0.2	0.9245
Forest x Grid x Nest	2	0.55	0.759	0	0.9982	1	0.6053
Bird v control	1	0	0.9694	0.74	0.3898	1.9	0.1671
Control v large	1	2.79	0.095	1.94	0.1635	2.9	0.088

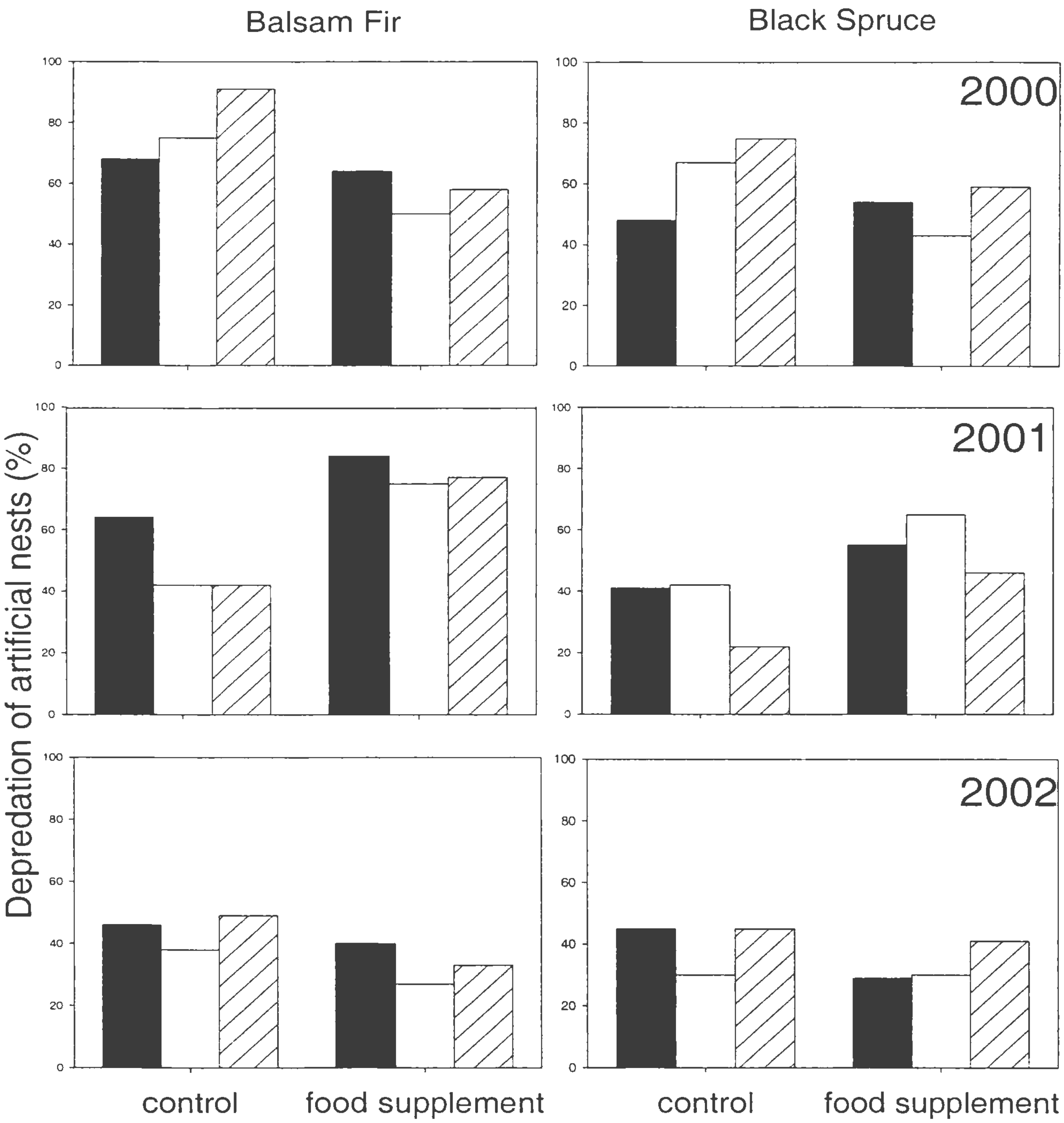

Figure 4.5. The influence of nest (bird = black, control = white, large = diagonal), on control and food supplemental grids in balsam fir and black spruce forest, 2000-2002.

Fig. 4.5). I consider the differences in nest predation between grid types to be biologically significant given the effect size, low levels of nest predation, and the small sample size.

For the secondary hypotheses, bird nests were depredated more in the balsam fir forest than in the black spruce forest (Appendix 4.4), but this difference was significant only in 2001 (2000: $\Delta G_1 = 1.57$, $p = 0.2108$, 2001: $\Delta G_1 = 8.23$, $p = 0.0041$, 2002: $\Delta G_1 = 0.45$, $p = 0.5021$). The absolute value of the difference in percent nest predation between food supplemental and control grids varied among years but was always greater in balsam fir (Fig.4.6).

4.5 DISCUSSION

Introduced red squirrels depredated more nests than any other identified predator in this study. Red squirrels were found at higher densities in black spruce than in balsam fir forests in two of the three years. There appears to be a general trend for nest predation to slightly increase with increased red squirrel density, but between forest differences may be more important. Concealment of the nests varied but had little influence on nest predation. In general, the support for Schmidt's model is equivocal since inter-annual variation in nest predation is large.

4.5.1 PREDATORS

Similar to other studies in Newfoundland (Lewis 1999, Lewis and Montevecchi, submitted a, b), and in boreal and coniferous forests (e.g. Darveau et al. 1997, Tewksbury

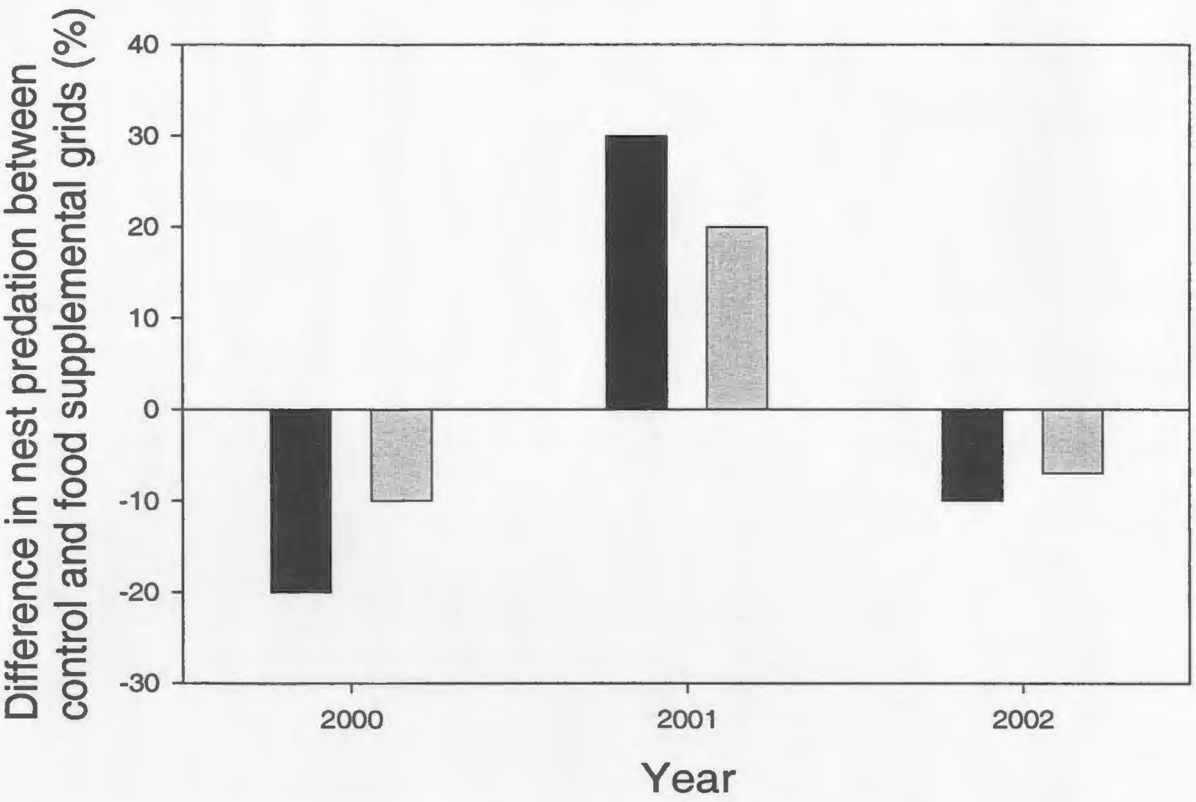

Figure 4.6. The percent difference in nest predation between control and food supplemental grids (% nest predation on control grid - % nest predation on food supplemental grids) in balsam fir (black) and black spruce (gray) forests, 2000 - 2002.

et al. 1998), I found that most artificial nests, where a predator was identified, were depredated by red squirrels. The ubiquity of red squirrels in forests, their arboreal nature, and low densities and richness of other nest predators likely contribute to the red squirrel being the dominant nest predator in Newfoundland (Lewis and Montevecchi submitted a). Similar to many studies using clay eggs (e.g. Martin and Joron 2003) and some with cameras (DeGraaf 1995), there were many unidentified predators, but many were probably red squirrels. Red squirrels will commonly remove both types of eggs and leave few remains (K. Lewis, pers. obs.). Other predators like red fox and weasel may also depredate nests but leave few remains. Red fox have been known to steal nest baskets from near the field station (K. Lewis pers. obs.), but red fox and short-tailed weasel densities are quite low precluding them as a major nest predator. Gray Jays leave obvious remains at nests, and are certainly an influence on tree nesting birds (Lewis 1999, Lewis and Montevecchi submitted a). Introduced red squirrels are the dominant nest predator in Newfoundland, and the role of other predators appears to be small (Lewis 1999, Lewis and Montevecchi submitted a, b).

4.5.2 RED SQUIRREL DENSITY

In 2000 and 2001, red squirrel densities were much greater in black spruce than in balsam fir forests, making these forests an appropriate place to examine the influence of broad differences in nest predator density on predation. These results for black spruce forests are consistent with other studies in Newfoundland (Reynolds 1997, West 1989), and other regions of North America (Rusch and Reeder 1978, Price 1994). To my knowledge, red squirrel densities have not been estimated in balsam fir forests. Studies conducted in balsam fir forests in Newfoundland have found extremely low red squirrel abundance, but this has been within a single watershed and may therefore, not be applicable to the rest of the island (Wren 2001, R. Thompson pers. comm.).

Differences in density among and within forests are likely related to cone production and abundance, the primary food of red squirrels (e.g. Smith 1968, Kemp and Keith 1970). Black spruce forests may provide more food than balsam fir for red squirrels in winter due to the semi-serotinous nature of black spruce cones, and greater cone production (Schooley 1976, Caron and Powell, 1989). Although balsam fir cones contain more seeds per cone and have larger seeds than black spruce cones (Burns and Hankala 1990), fir cones are perishable and contain large amounts of resin which may increase handling time for red squirrels and decrease its food value (L. Hermanutz, pers. comm.). Red squirrels seem to preferentially select black spruce cones and habitat over balsam fir (Brink 1965, Ferron et al. 1986, K. Tulk, pers. com.).

Red squirrel populations are relatively stable compared to other boreal species (Rusch and Reeder 1978, Boutin et al. 1995). The decline in red squirrel densities in black spruce forests in 2002 is likely a real, but temporary phenomenon, and not an artifact, because 1) my results in 2000-2001 are similar to Reynolds' (1997) in 1994-1995, 2) in 2002, I trapped one of Reynolds' grids and found much lower densities than he did, and 3) Wren (2001) found similar differences in red squirrel abundance between forest types. Abrupt but temporary declines in red squirrel populations have been documented in other studies (Kemp and Keith 1970, Keith and Cary 1991, Boutin et al.

1995, Stevens and Kennedy 1999), and may be influenced by the amount of overwinter food supplies (Kemp and Keith 1970). Variability in red squirrel densities among sites and years is probably influenced by numerous factors such as tree density (Sullivan et al. 1996), stand age (Sullivan and Moses 1986), and levels of insect infestation influence cone crops, that vary inter-annually among tree species. The complexity of this relationship could make it difficult to *a priori* predict red squirrel density within forests, and among years.

4.5.3 RED SQUIRREL DENSITY AND NEST PREDATION

Whether nest predator species richness increases with edges or habitat fragmentation, or if predators respond behaviourally, functionally, or numerically, is not often quantified (Chalfoun et al. 2002). Nevertheless, correlations between predator abundance and nest predation have been found for a number of predators (Chalfoun et al. 2002), including birds (Zanette and Jenkins 2000), birds and mammals (Cresswell 1997), snakes and birds (Patten and Bolger 2003), and sciurids (Rodewald and Yahner 2001, Martin and Joron 2003, Willson et al. 2003, cf. Marini et al. 1995). However, determining abundance is problematic, and many studies have calculated sciurid abundance using the auditory and visual censusing methods that are commonly used for breeding birds (i.e. point counts or transects; e.g. Rodewald and Yahner 2001, Martin and Joron 2003, Willson et al. 2003). While this approach is attractive due to its simplicity, it has not been shown to be a reliable method for censussing red squirrels (Flyger 1959, Bayne and Hobson 2000, K. P. Lewis, pers. obs.).

Therefore, this is one of the first studies to demonstrate a positive relationship between nest predation and red squirrel density using recognized trapping methods (see Schmidt et al. 2001b). Nest predation seemed to generally, but quite moderately increase with red squirrel density. Between forests and among years, a roughly 4 - 9 fold increase in density resulted a 15-20 % increase in predation (Fig. 4.5). Therefore, I accept the hypothesis that nest predation increases with the density of the dominant predator, but with several caveats.

Within forests, results vary, and could be due to low sample sizes and outliers. Furthermore, a positive relationship between predator abundance/density and nest predation is not the sole explanation for patterns of nest predation. Complex dynamics within the predator community can cause a negative relationship between nest predation and the density of small rodents (Schmidt 2001b), as can territory size among territorial predators (i.e. as territory size increases, there are more nests and hence a search image can be developed; Pelech 1999). Other factors such as a prey density (Gates and Gysel 1978), the richness of the predator community (Marini et al. 1995), increased incidental predation due to locally abundant food (Vickery et al. 1992, Schmidt et al. 2001a), and predator experience (Pelech 1999) may influence patterns of nest predation. More study of predator density and its relation with these other factors is warranted.

4.5.4 NEST CONCEALMENT AND NEST PREDATION

Differences in concealment among factors were minor and not biologically relevant. This is supported by the minor influence of concealment on nest predation in most years. However, there was a trend for nests to be more concealed in balsam fir than in black spruce forests, and nest predation was higher in balsam fir forests in all years although only significantly in 2001. These differences in concealment are likely due to differences in the understory. In Terra Nova National Park, nests were often hidden in the dominant shrub, kalmia, or under black spruce branches, which are both unpalatable to herbivores (Thomson and Mallik 1989). Kalmia was very rare on my study sites in Gros Morne National Park (K. Lewis pers. obs.), and where there is virtually no shrub layer due to browsing by moose and snowshoe hare (McLaren et al. in press). Nests were often hidden in less common natural cavities at the base of trees, fens, forbs, and coarse woody debris. These results suggest that there are more safe nest-sites in Terra Nova National Park, supporting the potential-prey-site hypothesis that search efficiency of the predator declines as the number of potential nest sites increases (Martin 1993, Filliater et al. 1994). The significant influence of concealment on nest predation in balsam fir forests in 2002 is likely an artifact of a few very visible nests being depredated. Therefore, while the sparse vegetation around nest-sites effectively blocks visual cues, it does not influence the predation of ground nests in these forests. I cannot reject the nest concealment hypothesis however, since vegetation may not inhibit olfactory cues.

Other research has found a relationship between nest predation and concealment of real nests (Crabtree et al. 1989, Martin 1993) and of artificial nests (Götmark et al. 1995, Cresswell 1997), while others have found no influence of nest concealment on real nests (Vicerky et al. 1992, Filliater et al. 1994, Götmark et al. 1995 Cresswell 1997, Brua 1999). These authors attribute the varying importance of concealment to the lack of safe nesting sites due to a diverse predator guild (Filliater et al. 1994, Brua 1999), trade-offs associated with a concealed nest and need for nesting birds to view their surroundings (Götmark et al. 1995), and nest defense (Cresswell 1997). My results are perhaps not surprising if red squirrels forage using olfactory cues (cf. Liebezeit and George 2002), or encounter nests incidentally (Vickery et al. 1992). More work is needed to determine how sciurids and other predators locate prey (Pelech 1999, Santisteban et al. 2002). I agree with Filliater et al. (1994) that "relationships between nest predation and nest-site features may exist, but may not be evident because the mechanisms influencing predation vary depending upon predator, and most nests are subject to a variety of predators."

4.5.5 SCHMIDT'S MODEL

4.5.5.1 Nest size

Although, small differences in concealment among nest types had little influence on levels of nest predation, Schmidt (1999) predicted that recognition costs should differ between nest characteristics and types. Willson and Gende (2002) found that large passerine nests were depredated more often than small ones. My findings were similar in 2000 and 2002 although these differences were not significant. This weak effect can be explained by the narrow range of parameters that I tested, a high probability of red squirrels encountering nests regardless of size, and that visual cues are likely of little importance for red squirrels and nest searching (cf. Burhans and Thompson 1998). Search cues and strategies for nest predators remain largely unexplored (but see Bowman and Harris 1980, Santisteban et al. 2002).

4.5.5.2 Nest defense

Passerines regularly guard and defend their nests, both actively and passively (e.g. Martin 1992, Cresswell 1997). Schmidt et al. (2001b) estimate that 60-75% of nest predation attempts by rodents (i.e. chipmunks and white-footed mice *Permoyscus leucopus*) may be repelled by passive or active parental defense. My results with red squirrels did not support these findings. There was no difference in predation between bird and control nests and although there was a trend for bird nests to be depredated more in balsam fir forests than in black spruce, this was only significant in 2001 (Appendix 4.4). Many decoys (i.e. passive defence), were apparently destroyed by red squirrels. The outcome would likely have been similar with real birds and active defense. Relatively large forest passerines such as Blue Jays cannot always defend their nests from red squirrels (W. Klenner pers. comm.), nor can Bicknell's Thrush (*Catharus bicknelli* K. McFarland pers. comm.), and red squirrels can kill adult song birds (Sullivan 1991, G. Stroud pers. comm.). Therefore, I reject the hypothesis that factors influencing passive nest defence will alter nest predation by red squirrels, or that differences in food levels between forests will affect the willingness of red squirrels to attack nests.

4.5.5.3 Supplemental food

These results are consistent with the hypothesis that the community dynamics of nesting birds may be influenced by higher and lower trophic levels and that effects between habitats may differ between years. Supplemental food caused a significant decrease in nest predation (10-20 %) in 2000, a significant increase (20 %) in 2001, and a non-significant, decrease (7-11 %) in 2002. These differences among years are likely not an artifact since the absolute value of differences in percent predation on control and food supplemental grids was always greater in balsam fir, and differs consistently across forest types through years (Fig. 4.6). The increase in predation in 2001, the lack of a more dramatic decrease in 2002, and the small differences between forests is surprising since food supplementation can radically alter red squirrel behaviour (W. Klenner pers. comm.) and populations in habitats with low density respond numerically more vigorously to food supplementation than habitats with high density (Klenner and Krebs 1991). Given the replicated reversal of treatments among years, these results suggest a strong year x site interaction, likely influenced by inter-annual variation in cone crops, which influence the densities and behaviours of red squirrel densities and predators.

The influence of mast seeding and fruit production have been shown to have far reaching effects in many different ecosystems (Ostfeld and Keesing 2000). Food supplementation has also been shown to divert red squirrels from specific food sources (Sullivan et al. 1993), and elevated levels of alternate food sources has been shown to reduce nest predation in other ecosystems (Dunn 1977, Hogstad 1995, Schmidt 1999, Vander Lee et al. 1999, Ackerman 2002, Schmidt 2003). Contrary to these studies, increased nest predation can result from incidental encounters as a result of increased alternate food sources (Vickery et al. 1992, Schmidt et al. 2001a). My results suggest that the influence of alternate food can change between years (see also Jones et al. 2002). Food may serve to alternately attract or distract predators from nest sites depending on the spatial proximity to songbird nests. Alternately, mast years are less predictable and occur less often in the boreal forest than in temperate deciduous forests (Schmidt 2003), leading to greater and less predictable variation among years. To understand the role of alternate food, we need to understand how the amount, spatial proximity, and predictability of the resource influences nest predators, and how inter-trophic level effects vary.

4.6 CONCLUSION

The purpose of this study was to evaluate hypotheses that describe the complex predator-prey relationship that is nest predation. One purpose of this study was to assess older hypotheses concerning nest predation, i.e. the nest predator density and nest concealment hypotheses. In this system, red squirrel density appears to have a modest but significant effect on nest predation. Nest concealment varied slightly among nest, grid and forest types, but its influence on nest predation appears to be slight, and the potential-prey-site hypothesis may be more applicable in these forests. The other purpose was to compare the explanatory power of these older hypotheses with a model based on foraging ecology (Schmidt 1999). It appears that the explanatory power of Schmidt's model may not be great in the boreal forests of Newfoundland where introduced red squirrels are the dominant predator. This may be due to nest predation being a largely incidental phenomenon, at least in northern forests (Vickery et al. 1992, Schmidt 1999). Schmidt (1999) assumes an actively foraging predator, but different predators may spend little time actually searching for nests but still have a strong effect due high densities and being able to access virtually all nests. Nevertheless, I feel that Schmidt's model is an excellent one for conceptualizing and exploring factors that influence nest predation and strongly encourage other authors to test this model with real nests, the Vickery-Gunn index (Gunn et al. 2000), and more diverse predator assemblages. As is often the case, departures from a model may be as informative as supporting evidence.

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Appendix 4.1. Summary of nest predators by forest, grid, and nest type from 2000-2002.

Year	forest type	grid	nest	bear	bird	mammal	mustelid	red squirrel	red squirrel ?	small mammal	Unidentified
2000	Balsam Fir	control	bird				1	6	1		5
			control					10	1		4
			large				1	5	2		2
		food	bird					7			
			control					6			3
			large					9	1		1
	Black Spruce	control	bird					2	1		11
			control					3			11
			large					7			11
		food	bird			2		3	1		8
			control					3			6
			large					3	1		9
			Total	**0**	**0**	**2**	**2**	**64**	**8**	**0**	**71**
2001	Balsam Fir	control	bird			2		5		1	8
			control					5	1		4
			large					3	1		6
		food	bird					10	3		8
			control					8			10
			large					12	1		7
	Black Spruce	control	bird		1	1		6			5
			control					7			6
			large					3			4
		food	bird			1		5	1		9
			control			1		6	2		11
			large					5			10
			Total	**0**	**1**	**5**	**0**	**75**	**9**	**1**	**88**

Appendix 4.1. Continued.

Year	forest type	grid	nest	bear	bird	mammal	mustelid	red squirrel	red squirrel ?	small mammal	Unidentified
2002	Balsam Fir	control	bird					11	3	1	
			control					8	1	1	
			large					15		1	1
		food	bird	1				7	1		
			control	1				3			3
			large					6		2	
	Black Spruce	control	bird					5			8
			control					2			5
			large					5			7
		food	bird			1		4			3
			control			2		2			3
			large			2		8			3
			Total	**2**		**5**		**76**	**5**	**5**	**33**

Appendix 4.2. Summary of average (± SD) adult red squirrel densities on grids (Appendix 4.1) in black spruce (bS) and balsam fir (bF) forests in 2000-2002. Density estimates were calculated using the robust design model with Huggin's estimator.

Forest	Grid	2000	2001	2002
balsam fir	Barter's Brook	0.92 ± 0.87	0.59 ± 0.32	1.42 ± 0.23
	Lower Barter's Brook			1.63 ± 1.56
	Lomond River Campground	1.82 ± 0.09	1.90 ± 0.49	2.29 ± 0.32
	Lomond River Road	0.81 ± 0.40	1.56 ± 0.20	1.76 ± 0.09
	South East Pond	0.91 ± 0.59	1.79 ± 0.76	0.70 ± 0.50
	Wiltondale			0.49 ± 0.69
	Mean	1.11 ± 0.47	1.46 ± 0.60	1.38 ± 0.68
black spruce	95-1			0.26 ± 0.37
	Arnold's Pond	2.64 ± 0.70	2.95 ± 1.52	0.93 ± 0.33
	Blue Hill North	2.11 ± 0.29	2.47 ± 1.41	2.08 ± 0.12
	Malady Head Campground	3.44 ± 0.34	2.53 ± 0.25	1.70 ± 0.30
	Malady Head Trail			1.05 ± 0.11
	Square Pond South	1.77 ± 0.29	1.50 ± 0.67	0.83 ± 0.44
	Mean	2.49 ± 0.73	2.36 ± 0.62	1.12 ± 0.65

Appendix 4.3. A summary of the mean (± SD) visibility values for all nest types in different forest and grid types. Top, side, and cardinal visibility values are given in order in each cell.

		Balsam Fir						Black Spruce					
Year	Nest	control			food supplement			control			food supplement		
	Treatment	Top	Side	Card	Top	Side	Card	Top	Side	Card	Top	Side	Card
2000	Bird	7 ± 7	2 ± 2		5 ± 9	2 ± 2		11 ± 8	2 ± 2		11 ± 8	1 ± 1	
	Control	8 ± 7	1 ± 1		10 ± 8	1 ± 1		9 ± 6	1 ± 1		6 ± 5	2 ± 2	
	Large	6 ± 6	1 ± 1		6 ± 8	1 ± 1		12 ± 7	1 ± 2		10 ± 7	1 ± 2	
	Total	7 ± 7	1 ± 1		7 ± 8	1 ± 1		11 ± 7	1 ± 2		9 ± 7	1 ± 2	
2001	Bird	2 ± 4	0 ± 1	13 ± 12	3 ± 6	0 ± 1	17 ± 13	6 ± 5	1 ± 1	26 ± 14	4 ± 5	1 ± 1	22 ± 14
	Control	3 ± 5	1 ± 3	11 ± 12	1 ± 3	0 ± 1	12 ± 14	4 ± 4	1 ± 1	21 ± 11	3 ± 5	1 ± 1	24 ± 15
	Large	2 ± 3	0 ± 0	13 ± 12	2 ± 3	0 ± 1	9 ± 8	5 ± 5	1 ± 1	21 ± 18	3 ± 5	1 ± 1	18 ± 10
	Total	2 ± 4	0 ± 2	12 ± 12	2 ± 4	0 ± 1	12 ± 12	5 ± 5	1 ± 1	22 ± 15	3 ± 5	1 ± 1	21 ± 13
2002	Bird	3 ± 4		15 ± 10	3 ± 4		12 ± 10	8 ±9		24 ± 14	3 ± 3		17 ± 14
	Control	3 ± 4		12 ± 11	3 ± 4		15 ± 11	5 ± 6		22 ± 17	2 ± 2		16 ± 9
	Large	2 ± 3		12 ± 9	5 ± 5		15 ± 10	4 ± 4		23 ± 16	6 ± 7		17 ± 14
	Total	3 ± 4		13 ± 10	4 ± 4		14 ± 10	6 ± 6		23 ± 16	4 ± 5		16 ± 12

Appendix 4.4. Summary of the proportion of preyed upon nests (percent in parentheses) by nest treatment, grid treatment, and forest type.

		Balsam Fir			Black Spruce			
Year	Nest	Control	Food	Total	Control	Food	Total	Grand Total
2000	Bird	13/19 (68)	7/11 (64)	20/30 (67)	14/29 (48)	14/26 (54)	28/55 (51)	48/85 (56)
	Control	15/20 (75)	9/18 (50)	24/38 (63)	14/21 (67)	9/21 (43)	23/42 (55)	47/80 (59)
	Large	10/11 (91)	11/19 (58)	21/30 (70)	18/24 (75)	13/22 (59)	31/46 (67)	52/76 (68)
	Total	38/50 (76)	27/48 (56)	65/98 (66)	46/74 (62)	36/69 (52)	82/143 (57)	147/241 (61)
2001	Bird	16/25 (64)	21/25 (84)	37/50 (74)	13/32 (41)	17/31 (55)	30/63 (48)	67/113 (59)
	Control	10/24 (42)	18/24 (75)	28/48 (58)	13/31 (42)	20/31 (65)	33/62 (53)	61/110 (55)
	Large	10/24 (42)	20/26 (77)	30/50 (60)	7/32 (22)	15/33 (45)	22/65 (34)	52/115 (45)
	Total	36/73 (49)	59/75 (79)	95/148 (64)	33/95 (35)	52/95 (55)	85/190 (45)	180/338 (53)
2002	Bird	15/33 (46)	10/25 (40)	25/58 (43)	14/31 (45)	9/31 (29)	23/62 (37)	48/120 (40)
	Control	12/32 (38)	7/26 (27)	19/58 (33)	10/33 (30)	9/30 (30)	19/63 (30)	38/121 (31)
	Large	16/33 (49)	8/24 (33)	24/57 (42)	14/31 (45)	13/32 (41)	27/63 (43)	51/120 (43)
	Total	43/98 (44)	25/75 (33)	68/173 (40)	38/95 (40)	31/93 (33)	69/188 (37)	137/361 (38)

5.0 Summary

Nest predation is an often studied, but still poorly understood, predator-prey interaction. Patterns and mechanisms of nest predation vary greatly among ecosystems. A theory that allows precise predictions to be made about the ecological patterns of predation does not yet exist, but recent papers have sought to remedy this situation (Schmidt 1999, Schmidt 2001a, 2001b). This lack of theory is due to the complexity, and perhaps, the unusual nature of nest predation. Eggs and nestlings are a temporally ephemeral food source, hence species cannot specialize as nest predators, and nest predation may be largely incidental (Vickery et al. 1992a, Schmidt et al. 2001a). Predation pressures differ regionally and local selection may be an important source of geographic variation in species interactions (Sanford et al. 2003). Furthermore, multiple predators can have risk reduction or risk enhancement effects on their prey (Sih et al. 1998).

In an attempt to understand the mechanisms underlying this complex relationship, I adopted a predator-based approach to the study of nest predation, rather than the more traditional approach of searching for correlations between nest predation and some feature of the habitat or nest characteristic. In general, this thesis demonstrates the functional significance of introduced red squirrels as the dominant nest predator in Newfoundland (Chapter 2). Red squirrel behaviour and patterns of nest predation are influenced by landscape processes and interactions with introduced herbivores (Chapter 3). Red squirrel density and alternate food influence nest predation but nest concealment and nest guarding are relatively unimportant in determining the fate of nests (Chapter 4). These results allow some predictions to be made about patterns of nest predation in Newfoundland, and these concepts can be profitably applied in other systems.

Most predator removal studies where bird nest are the prey are not designed to demonstrate the functional significance of different predators (Newton 1998), and most have been conducted on gamebirds to test the additive/ compensatory mortality hypothesis (Nichols et al. 1984), not additive/compensatory predation. In Chapter 2, I showed that in the two dominant forest types in Newfoundland, removal of introduced red squirrels dramatically lowered levels of nest predation, suggesting that the influence of red squirrels on predation is additive, especially on ground nests. Although many studies have shown that red squirrels are a primary nest predator, this is the first to demonstrate their functional role as a dominant nest predator. These results are probably applicable to most forested regions of the island and other forests with a limited nest predator assemblage (Martin and Joron 2003). I concur with Schmidt et al. (2001b) that understanding the relative importance of predators to nest predation is essential to understanding patterns of nest predation, and I introduced a conceptual framework for guiding such research.

At a landscape level, extreme habitat heterogeneity is characteristic of the Newfoundland landscape. It is critical to understand how this heterogeneity influences nest predation. The role of herbivory is rarely considered an important factor influencing avian assemblages and nest predation. In Chapter 3, I showed that nest predation was greater in forests than in adjacent gaps, and that this pattern mirrored red squirrel habitat use. This is the first study to suggest that disturbance-succession, succession-herbivory, plant-animal, and predator-prey interactions influence nest predation, and that herbivores indirectly influence nest predation by modifying the predator-prey interaction (Chapter 3).

Finally, the mechanisms by which nest predators drive nest predation patterns remain unclear (Chapter 4). To date, no study has simultaneously tested the nest predator density hypothesis, the nest concealment hypothesis, and a foraging theory model (Schmidt 1999). My results support the nest predator density hypothesis, but the effect appears to be modest. Visibility was not found to be an important aspect of nest concealment, which may not be surprising if squirrels search primarily using olfaction (Liebezeit and George 2002). Although trends often followed the predictions of Schmidt's model, few were statistically significant. Food seems to have a variable influence among years. I suggest that this model is useful for conceptualizing factors that influence nest predation and departures from the model are informative.

5.1 DIRECTIONS FOR FUTURE RESEARCH

Despite the enormous literature on nest predation, the complexity of the interaction insures that much remains to be explored. All three chapters could be substantially expanded in their depth and scope, and there is great opportunity for synthesis and utilization of new techniques.

Nest predation studies seeking to determine the functional role of different predators could benefit from adopting a more rigorous approach used in many predator manipulation studies. While many of these studies are conducted with small organisms (i.e. aquatic systems or terrestrial arthropods), a full factorial, predator removal study should be conducted (Sih et al. 1998). Findings from the rich literature on these smaller organisms should be used to guide research questions and methodologies. Ultimately, it would be useful to be able to predict if additive or compensatory predation will occur based on the characteristics of the predator and prey assemblages.

To this end, in regions where nest searching is difficult, I recommend targeted, species specific, large scale predator removals (Reitsma et al. 1990, Schmidt et al. 2001b) and estimates of breeding productivity with the Vickery-Gunn index (Vickery et al. 1992b, Gunn et al. 2000). This research should be implemented in Newfoundland. Red squirrels are very rare in the Main River watershed and other predators (weasel, marten, Gray Jays, R. Thompson pers. comm.) dominate the nest predator assemblage. In addition, the northerly expansion of eastern chipmunks on the island's west coast and the recent introduction and rapid expansion of red-backed voles may alter the current dynamic.

The framework suggested in Chapter 2 could also be profitably expanded to consider the role of primary and secondary predators at various vegetative strata. The functional role of predators likely varies in different vegetative strata (Schmidt 2002). A knowledge of foraging behaviour, access to vegetation strata, and the additive/compensatory effects could explain patterns of nest predation.

The research in Chapter 3 would ideally be conducted in a manner similar to Martin and Joron (2002), i.e. in a factorial design testing the effects of introduced herbivores and nest predators, but such conditions do not exist in Newfoundland. A possible way to explore the interaction of herbivores and red squirrels is to take advantage of hunting pressures in Newfoundland (similar to Casey and Hein 1984). Hunting of moose may increase with proximity to rural communities (B. McLaren pers. comm.), resulting in decreased herbivory pressure and an increased shrub cover in these areas.

Chapter 3 and Chapter 4 would have greatly benefited from direct tests of foraging decisions made by red squirrels using giving-up-densities (GUDS, Brown 1988, Schmidt et al. 2001a, 2001b). GUDs can be used to determine habitat quality, and related to nest predation (Schmidt et al. 2001a, 2001b), to examine the foraging costs associated with vegetative cover, and to test predictions of an incidental predation model (Schmidt 2001a). Despite attempts in all years, I was unable to conduct such a study due to inclement weather in 2001, and contrary to the previous two years, red squirrels did not forage in the seed trays in 2002. Most studies of nest predation that examine nest predator foraging ecology would benefit from employing this technique.

The research in Chapter 4 could be expanded by employing the Vickery-Gunn index (Vickery et al. 1992b, Gunn et al. 2000), a systematic monitoring of natural food levels, and surveys of other predators with track plates. The Vickery-Gunn index would allow testing of Schmidt's model among avian species, over a broader range of predators, and without the need for artificial nests. The effects of supplemental food may be confounded by natural food levels and should be addressed. In addition, Schmidt and Whelan (1999) proposed that spatial proximity of food can influence nest predators. The factors that influence whether food attracts, or distracts predators should be investigated.

Finally, there is very little work on how nest predators find nests (Bowman and Harris 1980, Pelech 1999, Santisteban et al. 2002). More research needs to be done to assess how predators find nests. Research on searching behaviour should then be integrated with field studies on foraging ecology (Schmidt 2001a, 2001b) to gain a better understanding of factors that influence patterns of nest predation.

Martin (1992) suggested a general theoretical framework integrating the influence of nest predation and food limitation on the evolution of life history traits. A model of nest predation that allows for prediction of pattern at the landscape scale is highly desirable. A general description of nest predation (P) could ultimately be

$$P = \sum d_i P_i S_i \qquad (1)$$

where d_i = density of predator i, P_i = the probability of locating a nest, and S_i = probability of successfully attacking a nest for predator i. Given the likelihood of generating the type of information required to fulfill equation 1 is extremely low, I suggest that many of the concepts presented in this thesis could be profitably unified, or unified with Schmidt's model. For example, predator removals could be conducted within the framework of Chapter 3. If real nest data or breeding productivity indices are available, Schmidt's model could be incorporated into this framework. There is a rich opportunity for examining the relative contributions of these factors to nest predation.

Newfoundland is an excellent laboratory for examining the influence of introduced species on a simple, boreal island ecosystem. A greater awareness of the direct and indirect effects of these introductions on the native biota is required, and could be the basis for interesting community and ecosystem ecology research.

5.2 CONSERVATION AND MANAGEMENT IMPLICATIONS

From the large numbers of predator manipulation studies, managers clearly desire to understand how controlling predator populations could influence avian populations and how best to control predator populations or behaviour. This study clearly demonstrates the need to know the functional role of individual predator species. This study suggests that removal of red squirrels in areas with a limited predator assemblage may be very effective at minimizing predation, while in areas with a diverse assemblage, removals may have limited influence (Reitsma et al. 1990). How to achieve removal of sciurids is less clear given their rates of colonization, trap shy animals, and potential public opposition. Use of supplemental food has proven successful in other studies (Crabtree 1988) and understanding how it can be best used to manipulate predator behaviour may be the easier than large scale live trapping.

The introduction of snowshoe hare and moose to Newfoundland have clearly had a large influence on vegetative composition and forest regeneration. Forests would likely regenerate were it not for the high populations of introduced herbivores. Moose are managed to maintain high population levels. Although moose are occasionally prey for bear and the recently immigrated coyote, humans kill the overwhelming number of moose in Newfoundland (McLaren et al. in press). In contrast, snowshoe hare have many predators and their populations are cyclic. If herbivore populations are maintained at high levels, herbivores will continue to play a large role in modifying the vegetation structure in areas where disturbance is patchy.

Maintenance of gaps by herbivores may also influence many songbird species. Few songbirds other than the ubiquitous White-throated Sparrows seem to frequent the insect kills (K. Lewis pers. obs., D. Fifield pers. com), although other birds use the alders and remaining spruce trees (K. Lewis, pers. obs.). Kalmia heaths are similarly species poor compared to adjacent forests, although they are frequented by Dark-eyed Junco, Hermit Thrush, and White-throated Sparrow (Lewis et al. 2000). The inhibition of forest regeneration by introduced herbivores may influence populations of songbirds that depend on balsam fir and hardwoods as well as early to mid-successional species. A possible way to inexpensively control herbivores and to simultaneously allow the vegetation to regenerate is to allow 1) a one time, localized cull of moose, or 2) extend the hunting season in areas affected by herbivory, during a low point in the snowshoe hare cycle.

These results of Chapter 4 are of importance to the nest predation literature in general.

An enormous amount of work has been done in the last 15 years on the influence of edges and habitat fragmentation (Paton 1994, Andrén 1995, Bender et al. 1998) that assumes, among other things, habitat loss creates areas of higher predator density which negatively influences breeding birds (Dijack and Thompson 2000, Chafloun et al. 2002). My results suggest that large increases in red squirrel density result in modest increases in nest predation. Nest predation may therefore increase slightly at edges where red squirrel densities can be higher than in interior forest (Pelech 1999, Anderson and Boutin 2002). Over a wide range of red squirrel densities, the result of habitat change for breeding birds are likely to come from habitat loss and not from elevated levels of nest predation near certain landscape features. Increased nest concealment through increased shrub cover may not decrease nest predation, but it may create more safe sites and habitat for nesting birds. This remains to be tested.

Most management strategies will have to be directed at manipulating red squirrel behaviour during the breeding season because, red squirrels have access to most nests, few passerine species can defend their nests from an attack, and red squirrel removals will be labour intensive and likely ineffective. Use of food, perhaps in conjunction with targeted, local live trapping of certain individuals, is perhaps the most promising approach for decreasing nest predation.

Newfoundland's distinctness from neighbouring landmasses and large number of endemic subspecies, coupled with the dominance of introduced mammals over the native biota are a concern for management and conservation. Introduced red squirrels and herbivores interact to influence nest predation and may influence local populations through nest predation, competition, and landscape change. Determining how best to moderate the direct and indirect effects of these introductions on the native biota in a socially acceptable manner is a considerable challenge.

5.3 CONCLUSION

Nest predation is a varied and unpredictable event, influenced by many factors. In Newfoundland, and much of the boreal forest, the red squirrel is the primary, and may often be the dominant predator. Nest predation in Newfoundland is influenced by herbivore modified succession which subsequently influences red squirrel behaviour. Finally, red squirrel density weakly influences nest predation and alternate food plays an important but variable role. This study indicates the need for a mechanistic understanding of the processes that influence an interaction as complex as nest predation, and argues for a holistic approach with rigorous study designs.

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