MECHANISMS REGULATING ECOLOGICAL RESPONSES TO RESOURCE PULSES
WITHIN CAVITY-NESTING BIRD COMMUNITIES

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
Doctor of Philosophy
in
THE FACULTY OF GRADUATE STUDIES
(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)
August 2012

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Abstract

Resource pulses may influence mechanisms that can regulate consumer populations directly through bottom-up effects on resource availability and indirectly via top-down effects of inter-specific interactions. Although these are well documented in food webs, the responses within nest webs (communities structured around nesting cavities in trees) have received little attention. Bark beetle (subfamily: Scolytinae) outbreaks represent food pulses that may lead to secondary pulses of nest cavities and increases in fecundity and competition among insectivores if excavating new nest cavities allows exploitation of novel habitats that increase reproductive output for both excavators and obligate secondary cavity nesters (SCNs), and if increased territory quality leads to greater energetic expenditures on territoriality. Using observational and experimental approaches, I examined how a large-scale outbreak of mountain pine beetle (*Dendroctonus ponderosae*) influenced the production of cavities, fecundity, and competition within nest webs at 30 sites in interior British Columbia, Canada, from 1995-2009. I used 1,018 nests of two species that varied in their ability to excavate cavities and specialize on bark beetles, Red-breasted nuthatch (*Sitta canadensis*; facultative excavator and bark beetle specialist) and Mountain chickadee (*Poecile canadensis*; SCN and generalist insectivore). I found that nuthatches excavated more cavities in lieu of using old cavities, maintained a constant clutch size throughout the breeding season (~6 eggs), and fledged up to 100% more young per nest, at sites and in years with increasing beetle abundance. Chickadee clutches were initiated earlier, mean clutch size increased from 5 to 7 eggs, and fledgling success doubled with a dual pulse of food and nest sites. I examined intra- and inter-specific territoriality by simulating conspecific and heterospecific territorial intrusions using 974 presentations with song playbacks, from 2004-2008. Chickadees,
although typically subordinate to nuthatches when competing for food, attacked all intruders more frequently (24% of 397 responses elicited) than nuthatches (8% of 372 responses). Both species showed increasing territoriality with increasing beetle abundance. Overall, my research suggested that species compensated both reproductively and behaviourally in response to resource pulses, and that plasticity in foraging and nesting behaviours can promote the resilience of wildlife communities in highly variable forest environments.
Preface

My thesis is a compilation of manuscripts written in collaboration with my supervisor, Dr. Kathy Martin. Chapter 2 has been submitted for publication: Norris, A. R. and Martin, K. Red-breasted nuthatch (*Sitta canadensis*) increases cavity excavation in response to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in interior British Columbia. Submitted 7 Dec 2011. Chapter 3 has been submitted for publication: Norris, A. R. and Martin, K. An insect outbreak reduces the costs of nest cavity production and increases reproductive output for an insectivore, and facultative excavator, red-breasted nuthatch *Sitta canadensis*. In Chapters 2 to 5, I designed experiments, collected and analyzed the data, and co-authored the manuscripts. K. Martin designed the initial long-term study and co-authored the manuscripts.
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Acknowledgments

I would like to first thank my supervisor, Dr. Kathy Martin. She has provided guidance, support, encouragement, and opportunities for new challenges that have greatly enhanced my career, and continues to be an outstanding mentor. My supervisory committee, Drs. Valerie LeMay and Daniel Weary contributed to the design, data analyses, writing, revising, and completion of my thesis. Drs. Jacob Goheen, Darren Irwin, and John McLean contributed ideas that improved the study design and early development of my thesis.

Many excellent field assistants collected data on the nest web project across the years, including Dayani Gunawardana, Meghan Marjanovic, Isabelle and Marius Behret, Haley Kenyon, Amanda Edworthy, Marty Mossop, Alicia Newbury and Natasha Knight. They provided friendship, and taught me essential skills in cooking and empathy. My husband, Patrick Robinson, helped to manage fieldwork and has been a sounding board for many of the ideas in my thesis. I am grateful for my family and friends, Margaret Norris, Sheree and Mark Carrier, Gail and Tim Norris, Felice Griffiths, Nicola Freeman, Delaine and Jeremy Coleman, Jason, Garth and Alyssa Norris, Emily and Taj Carrier, and Alexis Foley-Norris, who provided encouragement, field accommodations and volunteered to assist in data collection.

My thesis benefited from discussions and/or comments from: Kristina Cockle, Katie Aitken, Mark Drever, Alaine Camfield, Matthew Tomlinson, Alice Boyle, Amy Koch, Krista DeGroot, Karen Wiebe, Peter Arcese, Pierre Drapeau, Tomasz Wesolowski, Hugo Robles Diez, Tomás Ibarra, Beth MacDonald, and members of Vertebrate Ecology Discussion Group at UBC.

My study was supported by many generous individuals and sponsors. Daryl Cockle built and maintained the cavity monitoring equipment. I received a Post-graduate Doctoral Scholarship
from the Natural Sciences and Engineering Research Council of Canada (NSERC), a Four Year Doctoral Fellowship and a Pacific Century Graduate Scholarship from the University of British Columbia, and research grants from the Forest Investment Account Forest Science Program (Graduate Student Pilot Project and Mountain Pine Beetle Initiative Graduate Research Fund), the Southern Interior Bluebird Trail Society, and a Junco Technologies Award from the Society of Canadian Ornithologists and Bird Studies Canada. Funds from NSERC, Environment Canada, including the Space for Habitat project and Science Horizons Intern Program, and Tolko Limited were provided to Dr. Martin.
Chapter 1. General introduction

Infrequent, large, abrupt increases in resource availability, resource pulses, regulate many communities in terrestrial and aquatic ecosystems, through both bottom-up and top-down processes (Ostfeld and Keesing 2000). Examples within terrestrial systems include seed or fruit masting (Kelly 1994, O’Donnell and Phillipson 1996, Wolff 1996, Jedrzejewski and Jedrzejewski 1998, Gonzalez and Donoso 1999), El Niño rainfalls in arid systems (Polis et al. 1997, Grant et al. 2000, Meserve et al. 2003, Letnic et al. 2005), hurricanes that result in litterfall in tropical forests (Lodge et al. 1994, Woolbright 1996), and insect outbreaks (Carlton and Goldman 1984, Ito 1998, Haney 1999, Yang 2004, Hogstad 2005). Aquatic resource pulses include marine upwelling events (Bode et al. 1997), and occurrences across aquatic and terrestrial systems include large marine subsidies to terrestrial environments (e.g. whale carcasses; Rose and Polis 1998), and storm-driven terrestrial subsidies, such as organic nutrients, to aquatic systems (Burkholder et al. 1997). These resource pulses can permeate through multiple levels of food webs causing changes in community dynamics, population densities and behavioural interactions among consumers (Ostfeld and Keesing 2000, Yang et al. 2008). It is imperative to understand the direct and indirect effects of resource pulses for effective community-wide conservation of wildlife populations (Yang et al. 2008).

Major resource pulses in temperate terrestrial ecosystems are seed masting events and insect outbreaks (Ostfeld and Keesing 2000). Many species can detect irruptions in seed production and insect abundance, and show responses at the population level (Newton 1994, Koenig and Knops 2001, Boutin et al. 2006). Worldwide, approximately 60% of 8600 bird species with known foraging habits are partly or largely insectivorous (Mayr and Amadon 1951); thus, insect
outbreaks can elicit greater reproductive responses as many vertebrates switch to an insectivorous diet when breeding (Morse 1971). In North American forests, population- and community-level changes have been documented in response to outbreaks of cicadas (Magicicada spp; Rosenberg et al. 1982, Yang 2004), moths and butterflies (Lepidoptera spp; Morris et al. 1958, Morse 1978, Elkinton et al. 1996, Koenig et al. 2011), and bark beetles (Scolytinae; Koplin 1969, Otvos 1979, Romme et al. 1986, Drever et al. 2008). However, none of these studies examined the effects of insect outbreaks at multiple levels of resource constraints within a community structured around non-food resources. A recent outbreak of mountain pine beetle (Dendroctonus ponderosae) was the largest on record for North America and the province of British Columbia, Canada (Eng et al. 2005). The beetle outbreak resulted in changes in population densities of many forest-dwelling vertebrates (Drever et al. 2008, Norris and Martin 2010), and thus provided an ideal natural experiment in which to examine the effects of forest resource pulses on a wildlife community that is structured around multiple resource constraints.

Forest bird communities are often structured hierarchically around complex inter-specific interactions of species that excavate tree cavities and other species that secondarily use those nest cavities, analogous to food webs (nest webs; Martin and Eadie 1999). Secondary cavity nesters, which include some nest predators, do not excavate new nest cavities but rely primarily on excavators, whereas a few species, facultative excavators, show plasticity in excavation tendencies (Aitken et al. 2002). As many excavators are insectivores, large-scale insect outbreaks can lead to dual pulses in food and nest sites (Edworthy et al. 2011). Many other species in the nest web are also insectivores; thus, community-wide pulses in food can lead to increases in population densities of competitors and predators. Temporal fluxes in resource availability and population densities of community members can change the strength of inter-specific interactions
within the community, and the regulatory mechanisms of populations, influencing the fecundity of, and competitive interactions among, cavity-dependent insectivores (Aitken and Martin 2008). Studying insect outbreaks within the context of nest webs allows examination of direct and indirect effects of inter-specific interactions, critical information required in the advancement of knowledge on resource pulses and community ecology (Agrawal et al. 2007, Yang et al. 2010).

The Effects Of Food Pulses On Nest Site Limitation And Predation Risk

Food limitation is often found to be the primary factor affecting breeding phenology, clutch size, and nest success in birds (Lack 1947, 1954, Newton 1998). In temperate climates where breeding seasons are limited to only a few months annually, and insect emergence occurs in one peak during the season, insectivores lay as many eggs as they expect to be able to feed, and the peak in nestling requirements often coincides with the pulse in insect availability (Lack 1954, Newton 1998). Nestlings that hatch earlier in the season are able to accumulate more mass and gain more experience foraging and avoiding predators before the winter when mortality is highest (Martin 1987). Increases in food supply may advance reproduction, leading to increased clutch size, number of fledglings, survival of juveniles, and propensity to initiate a second brood (Martin 1987, Arcese and Smith 1988, Stuart Simons and Martin 1990). Nest success can also increase with food availability, as adults spend less time foraging and more time defending nests from predators, the primary source of nest mortality in most species (Lack 1947, Martin 1993). If food pulses are shared with nest predators that are able to switch from foraging on bird nests to the pulse resource, nest success may not change or may even increase with abundant predator populations (Ostfeld and Keesing 2000). However, conflicting evidence shows that increases in predator populations can suppress prey reproduction regardless of a superabundant food supply.
(Schmidt and Ostfeld 2008). Thus, insect outbreaks can influence the fecundity of insectivores both directly through reproductive output and indirectly through changes in nest predation risk.

Suitable nest tree cavities are essential to reproduction, and often have important fitness consequences in cavity-nesting birds (Newton 1998, Martin and Eadie 1999). Under the nest site limitation hypothesis, species that can excavate their own cavities are less constrained in territory selection by cavity availability, and may exhibit greater flexibility in nest placement (Martin 1993, Norris and Martin 2008). In comparison to cavities excavated in previous years, newly excavated cavities may harbour lower parasite loads and be less prone to predation as predators are less familiar with new cavities (Martin 1995). On the other hand, when species use old cavities rather than excavate fresh cavities, the energy required to excavate may be allocated instead to breeding effort, and cavity volume tends to increase with time after excavation, thus non-excavators often produce earlier, and larger clutches than excavators (Martin 1993, Mönkkönen and Martin 2000, Aitken et al. 2002, Wiebe et al. 2007). New cavities can allow greater flexibility in nest placement and alleviate competition for existing cavities, and may offer lower nest predation risk and parasitism rates, but old cavities are larger and can allow greater reproductive output in a breeding season.

Facultative excavators show plasticity in their use of old and new cavities, and, as a result, may respond to temporal or spatial changes in resource availability and community dynamics to optimize fitness benefits (Mönkkönen and Martin 2000, Wiebe et al. 2007). Facultative excavators may use old cavities to lay earlier, and larger clutches to exploit dual pulses in food and nest sites (Martin 1993, Mönkkönen and Martin 2000, Wiebe et al. 2007). However, food pulses that lead to increased population densities of cavity consumers and nest predators can result in increases in both competition for cavities and nest predation risk, which can result in
reductions in reproductive success for facultative excavators (Lack 1947, Martin 1995, Ghalambor and Martin 2000, Ostfeld and Keesing 2000, Aitken and Martin 2012). Edworthy et al. (2011) found that a food pulse led to increased breeding densities but not fecundity in obligate excavators (woodpeckers; Picidae). Excavation may be favoured over competition for old cavities, particularly when predation risk is high, but the energy required to excavate early in the breeding season may prevent earlier breeding and larger clutches. Facultative excavators may use either old cavities to maximize reproductive output or new cavities to avoid competition and minimize nest predation in response to food pulses shared with predators. Despite the major differences in cavity acquisition strategies, there has been little examination of the factors influencing the patterns of cavity excavation within facultative excavator species.

For secondary cavity nesters, a limited supply of nest sites may force individuals to nest in areas of higher nest predation risk, and adopt other strategies to avoid nest predation. Some species modify their behaviour at the nest to reduce risk of detection by predators (Fontaine and Martin 2006, Rangel-Salazar et al. 2008), and others choose cavities with characteristics that reduce predation risk. For example, cavities with smaller entrances may restrict larger-bodied predators, such as squirrels (Wesołowski 2002), and nests higher above the ground are often safer from terrestrial predators such as snakes and rodents (Nilsson 1984, Albano 1992, Fisher and Wiebe 2006). Although encounters with predators can be difficult to avoid during resource pulses that are shared with predators (Schmidt and Ostfeld 2008), predators can also switch to foraging on the pulsed resource rather than bird nests (Ostfeld and Keesing 2000, Mahon and Martin 2006). Thus, community-wide resource pulses may reduce nest predation risk for secondary cavity nesters directly by increasing food availability for foraging pairs to increase nest vigilance,
and indirectly if the availability of safer cavities increases, or predators switch to consuming the pulsed resource.

**Intra- And Inter-specific Competition For Territories**

Resource pulses may influence intra- and inter-specific interactions differently, depending on the mechanisms regulating competition for territories. Direct competition both within and between species may increase if resource pulses provide potential reproductive benefits for individuals to defend high quality sites (Territory Investment Hypothesis; TIH; Brown 1964, Fretwell and Lucas 1970). Indirect competition may decrease between species but increase within species, by expanding niche breadth, and reducing inter-specific dominance of resource specialists over generalists (Ecological Niche Hypothesis; ENH; MacArthur 1958, Morse 1974, Chase and Leibold 2003). Finally, direct and indirect competition within and between species may decrease if individuals use the presence of conspecifics (Stamps 1988) or heterospecifics with similar habitat requirements (Mönkkönen et al. 1990) to assess territory quality in unpredictable environments (The Competitor Attraction Hypothesis; CAH). Inter-specific dominance hierarchies can be reversed when dominants invade breeding territories of subordinates (Morse 1976), but the effects of spatial and temporal variation in resource supply on the behavioural mechanisms underlying these reversals are not known. Empirical studies of the effects of resource pulses on changes in the nature and strength of inter-specific relationships may help to fill key gaps in our understanding of functional processes in community ecology (Agrawal et al. 2007).
Thesis Objectives

The goal of my thesis research was to examine how a dual resource pulse of food and nest sites influences the mechanisms regulating populations and inter-specific interactions within nest webs in interior British Columbia, Canada (Figure 1.1). Specifically, I tested whether and how 1) the mountain pine beetle outbreak influenced the decision to excavate in a facultative excavator (Chapter 2), 2) the beetle outbreak influenced the reproductive constraints associated with excavating new cavities in a facultative excavator (Chapter 3), 3) the dual resource pulse in food and nest sites influenced fecundity for an obligate secondary cavity nester (Chapter 4), and 4) competition for territories between a facultative excavator and an obligate secondary cavity nester that share foraging and nesting niches, changed with pulses in food and nest sites (Chapter 5). I predicted that the dual resource pulse in food and nest sites would result in direct and indirect effects on fecundity for nuthatches and chickadees via changes in resource availability, nest predation by squirrels, and/or intra- and inter-specific interactions (Figure 1.2).

Study Area

Fieldwork was conducted at 30 mixed coniferous-deciduous forest stands near the city of William’s Lake, British Columbia, Canada (51°52’N, 122°21’W; Figure 1.1). Predominant coniferous tree species were Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*), and hybrid spruce (*Picea glauca* x *engelmannii*), and the predominant deciduous tree was trembling aspen (*Populus tremuloides*; Meidinger and Pojar 1991). The sampling sites ranged from 15 to 32 ha (one 7-ha site) in size, and varied in composition from continuous forest to five sites that were comprised of a series of ‘forest groves’ (0.2 to 5 ha) within a grassland matrix (Aitken et al. 2002). My study was in conducted
collaboration with a long-term study on nest webs (1995-2011), and I used data from 1995-2009. Within the larger nest web community, I focused on a sub-web of small species that showed overlap in nesting and foraging habits (Martin et al. 2004; Table 1.1). I provide additional details on the study area in individual data chapters.

**Thesis Overview**

In Chapter 2, I examined how the abundance of mountain pine beetle and associated changes in population densities of conspecifics and a nest predator, red squirrel (*Tamiasciurus hudsonicus*) influenced the probability of excavation by a bark insectivorous, facultative cavity excavator, Red-breasted nuthatch (*Sitta canadensis*), from 1995-2009. I used generalized linear models to examine how variation in excavation rates (i.e., whether a nest was freshly excavated in the year that it was used) could be explained by variation in the densities of beetle-infected pine trees, conspecifics, and squirrels detected at the site in the year that the nest was found. I found that the probability of excavation increased as nuthatch population densities increased in beetle abundant patches. I discussed the implication that excavation ability promotes exploitation of novel habitats during insect outbreaks in disturbance-driven forests.

In Chapter 3, I examined whether nuthatch pairs experienced any reproductive consequences as a result of the shift in excavation strategies and nesting habitat. Specifically, I determined how the increases in the propensity to excavate new cavities, and how the densities of conspecifics and predators influenced the fecundity of Red-breasted nuthatch. I found that nuthatches laid larger later clutches, and fledged a greater number of nestlings, with increases in beetle abundance. However, the number of fledglings declined with increases in squirrel densities. I tested the food, nest site, and nest predation hypotheses, and discussed how multiple
constraints to breeding may interact with each other in species exhibiting plasticity in excavation behaviour. Thus, facultative excavators exhibited variation from the usual avian relationship between nesting phenology and clutch size in response to the beetle outbreak, such that increasing latency of nest initiation did not result in smaller clutches despite an increased expenditure of energy required for excavation.

Given that excavation allowed for the positive reproductive responses to the beetle outbreak, I then examined whether a species that is unable to excavate could exhibit plasticity in other reproductive strategies to benefit from the beetle outbreak, such as adjusting nest predation risk. In Chapter 4, I examined how fecundity in the secondary cavity nesting species, mountain chickadee, was influenced by changes in the availability of mountain pine beetle and a lepidopteran, western spruce budworm (Choristoneura occidentalis) and associated increases in nest cavity availability and predator densities. Also, I compared the fecundity of pairs in cavities produced by larger-bodied excavators to those produced by small-bodied excavators, to examine how cavity entrance size influenced reproductive success. Then, I examined how beetle abundance and nest predator densities influenced the plasticity in the parental investment behaviour (parental feeding trips). I found that chickadees laid earlier, larger clutches at sites and in years with increasing beetle abundance. The probability that pairs fledged at least one nestling increased with beetle abundance, but declined with squirrel densities. Also, nest survival increased in smaller-sized cavity entrances, such that nests in cavities excavated by the small-bodied nuthatches and downy woodpeckers (Picoides pubescens) had higher survival than those in the larger-bodied red-naped sapsucker (Sphyrapicus nuchalis) cavities. Finally, I found that chickadee parents increased the number of feeding trips as the brood size increased, but not at sites and in years with high squirrel densities. I discuss the implications of increased food supply
on the plasticity in predator avoidance strategies in nest cavity choice and nest vigilance behaviour in a species limited by nest site availability.

Having examined the fecundity implications of the beetle outbreak for two species that occupy similar ecological niches, in Chapter 5, I examined how behavioural mechanisms regulated coexistence within and between species. Specifically, I evaluated the evidence for intra- and inter-specific competition among nuthatches and chickadees by simulating territorial intrusions, using intruder presentations with playbacks, during 2004-2008. I used generalized linear mixed-effects models to show how beetle abundance influenced the response to both conspecific and heterospecific intruders. I found that both species showed increasing aggression to territorial intruders with increasing beetle abundance, but at highest beetle abundance, the typically subordinate species, chickadee, shifted to an inter-specific resource defence strategy, and became more dominant to nuthatch intruders than to conspecifics. I then reviewed the evidence for each of the competing hypotheses that are used to describe competition for territories according to resource specialization at the nesting and foraging guilds. I concluded that resource specialists (mountain chickadee) dominated generalists (red-breasted nuthatch) at the nesting guild, and that both species increased defense of high quality territories, supporting the Territory Investment Hypothesis. Finally, I discuss the implications of resource pulses on the behavioural interactions regulating coexistence within resource-structured vertebrate communities.

In Chapter 6, I discuss the major implications of insect outbreaks on forest vertebrate communities, and the generality of direct and indirect effects of resource pulses on communities structured around multiple resource constraints. I identified critical gaps in knowledge and provided recommendations for future research on resource pulses and nest web ecology. Future
work should refine specific predictions outlined in my thesis, of species- and community-level responses to resource pulses, and should test these predictions in other systems to broaden the generality of my conclusions. As most research on resource pulses examines food webs in northern temperate forests, further work on nest webs in southern temperate forests to increase the depth and breadth of my research is required. As one potentially productive avenue of future work on community dynamics and resource pulses, I identified a group of poorly understood cavity-nesting species found in Chilean Temperate forests that have similar foraging and nesting requirements to nuthatches and chickadees in North America. To achieve generality of mechanisms and insights, I propose future research to compare the effects of resource pulses on nest webs between North and South Temperate forests.
Table 1.1. Cavity-nesting species that are known to influence nesting ecology of Red-breasted nuthatch and/or Mountain chickadee, through the production of nest sites, similarities in foraging preferences, or nest predation, and the total number of nests found in the study, across 30 sites in interior British Columbia, Canada, from 1995-2009.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nesting guild</th>
<th>Foraging guild</th>
<th>Total nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-naped sapsucker</td>
<td>Excavator</td>
<td>Sap and insects</td>
<td>496</td>
</tr>
<tr>
<td><em>(Sphyrapicus nuchalis)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Downy woodpecker</td>
<td>Excavator</td>
<td>Bark insectivore</td>
<td>108</td>
</tr>
<tr>
<td><em>(Picoides pubescens)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-capped chickadee</td>
<td>Excavator</td>
<td>Foliage insectivore</td>
<td>80</td>
</tr>
<tr>
<td><em>(Poecile atricapillus)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-breasted nuthatch</td>
<td>Facultative excavator</td>
<td>Bark insectivore</td>
<td>420</td>
</tr>
<tr>
<td><em>(Sitta canadensis)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountain chickadee</td>
<td>Secondary cavity nester</td>
<td>Foliage insectivore</td>
<td>598</td>
</tr>
<tr>
<td><em>(Poecile gambeli)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red squirrel</td>
<td>Secondary cavity nester</td>
<td>Generalist predator</td>
<td>116</td>
</tr>
<tr>
<td><em>(Tamiasciurus hudsonicus)</em></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1.1. Map of British Columbia, with the study area shown in the shaded box on the inset, and a satellite image of study area clusters (round symbols) surrounding Williams Lake (star symbol). Numbers in brackets indicate the number of study sites at each cluster location.
Figure 1.2. A group of small-bodied cavity nesters that vary in their ability to excavate cavities and specialize on bark beetles, red-breasted nuthatch, a facultative excavator and bark beetle foraging specialist (left), mountain chickadee, a secondary cavity nester and bark beetle generalist forager (right), and red squirrel, a secondary cavity nester and generalist-foraging predator. A bark beetle outbreak is predicted to increase food and nest site availability (block arrows) and influence mechanisms regulating population dynamics and inter-specific interactions (line arrows).
Chapter 2. Red-breasted nuthatch (*Sitta canadensis*) increases cavity excavation in response to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in interior British Columbia

Suitable nest tree cavities are essential to reproduction and often have important fitness consequences in cavity-nesting birds (Martin 1993, Newton 1998). Under the nest site limitation hypothesis, species that can excavate their own cavities are less constrained in territory selection by cavity availability and may exhibit greater flexibility in nest placement (Martin 1993). On the other hand, when species use old cavities rather than excavating fresh cavities, the energy required to excavate may be allocated to breeding effort instead, and non-excavators often produce clutches that are earlier and larger than excavators (Martin 1993; Mönkkönen and Martin 2000, Wiebe et al. 2007). However, predators may be more familiar with old cavities, which may also tend to harbour greater parasite loads (Martin 1995). Thus, new cavities can allow greater flexibility in nest placement and alleviate competition for existing cavities and may offer lower nest predation risk and parasitism rates, but old cavities can allow greater reproductive output in a breeding season.

Facultative excavators show plasticity in their use of old and new cavities, and, as a result, may respond to changes in resource availability and community dynamics to optimize fitness benefits (Mönkkönen and Martin 2000; Wiebe et al. 2007). Major increases in food availability or food pulses leading to high breeding population densities may result in further constraints on secondary resources (Ostfeld and Keesing 2000). At the community level, if high population densities of competitors and predators lead to higher competition for cavities and higher nest predation risk, then excavation may be favoured over competition for old cavities. Thus, food and nest site availability, and nest predation risk may affect the decision to excavate differently
(Figure 2.1), and, yet, there has been limited examination of the factors influencing the patterns of cavity excavation within facultative excavator species.

In temperate forests, periodic large-scale insect outbreaks can result in food pulses for insectivores (Morse 1971, Dickson et al. 1979). Red-breasted nuthatch (*Sitta canadensis*; hereafter nuthatch) is one of the most common facultative excavators and bark-foraging insectivores in North America, and is, thus, an ideal species in which to examine the effects of bark beetle (*Scolytinae*) outbreaks on excavation behaviour (Ghalambor and Martin 1999). Nuthatch is considered a weak excavator and shows preference for decayed deciduous snags as nest substrates, which are often in limited supply in mixed coniferous-deciduous stands in British Columbia, Canada (Steeger and Hitchcock 1998, Martin et al. 2004). Within mixed coniferous-deciduous stands, trembling aspen (*Populus tremuloides*, hereafter aspen) comprises 95% of all nest tree species used by cavity nesters (Martin et al. 2004). However, in this study, aspen represents only 15% of trees available in the study area (Aitken and Martin 2007).

In an earlier study, I found that nuthatches excavate new cavities about 50% of the time, but they may prefer to use old cavities when cavity availability is high and excavate when cavity supply is low (Norris and Martin 2010). An insect outbreak within a nest web can lead to either: 1) increases in population densities of several or all cavity-using insectivores, and subsequently, increased competition for cavities (Drever et al. 2008, Aitken and Martin 2012); 2) increases in nest tree availability via increased availability of decayed beetle-infected trees (Steeger and Hitchcock 1999); or 3) increases in cavity availability via increased population densities of cavity-excavating insectivores (Norris and Martin 2010, Edworthy et al. 2011). Thus, during insect outbreaks, facultative excavators may either: 1) excavate new cavities to avoid competition for cavities, and exploit the dual pulse of food and snag availability when cavity supply is low; or
2) capitalize on higher reproductive output offered by the food pulse by using existing cavities when abundant.

Nuthatch populations are irruptive and can increase in response to large-scale increases in food and nest site availability (Ghalambor and Martin 1999, Norris and Martin 2010, Aitken and Martin 2012). I observed population irruptions in nuthatches that corresponded with a large-scale, community-wide food pulse of mountain pine beetles (*Dendroctonus ponderosae*; Norris and Martin 2010) that affect lodgepole pine (*Pinus contorta var. latifolia*) trees, primarily. Also coinciding with the beetle outbreak, densities of a common cavity nest predator, red squirrel (*Tamiasciurus hudsonicus*) increased (Mahon and Martin 2006, Norris and Martin 2010). During the beetle outbreak, nuthatches shifted nest-patch selection away from areas of high nest site availability, primarily in aspen trees, to those of high beetle availability (beetle-infected pine trees; Norris and Martin 2008). This suggests that individuals traded off high cavity availability for high food availability during the beetle outbreak, when generalist nest predator densities were high. In this chapter, I examine how the beetle outbreak and subsequent changes in population densities of competitors and predators influenced the excavation patterns in red-breasted nuthatch. I predicted that high competition for cavities and high nest predator densities in areas of high beetle abundance would result in red-breasted nuthatch excavating a greater proportion of cavities.

**Methods**

Fieldwork was conducted within the warm and dry Interior Douglas-fir biogeoclimatic zone of central British Columbia, Canada (Meidinger and Pojar 1991). The study area comprises mixed coniferous-deciduous forest, with Douglas-fir (*Pseudotsuga menziesii var. menziesii*),
lodgepole pine (hereafter pine), and white and Englemann hybrid spruce (*Picea glauca* x *engelmannii*) as predominant coniferous species and with aspen as the predominant deciduous species. Seventeen of the 30 study sites were located near Riske Creek, 40 km west of the City of Williams Lake, and 13 sites were near Knife Creek, 20-40 km east of Williams Lake (52°14’N, 122°12’W). Sampling sites (mostly 15 to 32 ha in size) varied in composition from conifer-dominated continuous forest with aspen-leading edges to five sites that were a series of aspen-dominated ‘forest groves’ (0.2 to 5 ha) within a grassland matrix. Additional study area details are given in Martin and Eadie (1999) and Aitken et al. (2002).

**Nest monitoring**

Field data were collected from May through July at 30 sites, during 15 years, 1995-2009. I conducted systematic nest searches, point count surveys, and vegetation surveys to monitor breeding activity, abundance, and habitat associations of all cavity-nesting species. I found nests by visually inspecting previously occupied cavities and by following and observing breeding behaviours of adults and pairs at all sites. I used a video camera cavity monitoring system (starting in 2005), or a mirror and halogen flashlight from the ground or a ladder, to inspect cavities and monitor nests in natural cavities (formed by excavators or decay), approximately every 4-7 d. Nests were considered active by the presence of eggs, or chicks. I noted the cavity type as freshly excavated in the same year as breeding (where I observed an adult excavating earlier in the breeding season, or fresh woodchips below the cavity entrance or at base of the nest tree) or not (formed in a previous year; where I monitored the cavity in a previous year, or the cavity entrance appeared worn). I measured nest tree characteristics including: tree species; the distance between the nest tree and the nearest forest edge where the forest was adjacent to a
grassland opening, a clearcut, or a lake; the cavity height above ground; and the decay stage of
the nest tree (decay classes: 1: was a live, healthy tree; 2: a live tree with visible sign of bark
boring insects and/or fungal decay; and 3-8: standing dead trees in progressive states of decay;
Thomas et al. 1979). I excluded two nuthatch nests shared with another cavity-nesting bird,
mountain chickadee (*Poecile gambeli*; Robinson et al. 2005) from all analyses.

**Nuthatch and squirrel population densities**

Point count surveys were conducted to estimate population densities of red-breasted
nuthatches and red squirrels at 27 sites, during 1995-2009. In continuous forest sites, point count
stations were spaced evenly in a 100 x 100 m grid starting at a grassland or wetland edge and
extending into the forest. In forest groves where trees were patchily distributed, I placed point
count stations at least 100 m apart. From 0500-0930 hours, I recorded the species, and number of
individual birds and squirrels detected within 50-m radius 6-minute point counts at each station
(mostly 15-32 stations site\(^{-1}\)). I surveyed 425 stations across 27 sites three times (rounds) each
year. The three additional sites were not surveyed using point counts, but were used for nest and
vegetation monitoring. Further details of population monitoring methods are provided in Martin
and Eadie (1999) and Drever et al. (2008). I divided the total number of individuals observed at
all point count stations on all rounds by the total number of point counts and rounds conducted to
obtain estimates of mean individuals ha\(^{-1}\) for each site and year.

**Beetle abundance**

During the study period, an outbreak of mountain pine beetles progressed over all sites,
with incidence of beetle attacks on pines increasing sharply after 2002 (Drever et al. 2009). By
2005, over 95% of the mature pine trees (40% of the trees on the sites) were dead (Edworthy et al. 2011). However, the onset of beetles showed some temporal and spatial variation with respect to site level characteristics. To determine habitat associations of nests, 0.04-ha circular vegetation plots were established and centered at each active nest and point count station during 1995-2009. For all trees ≥12.5 cm diameter at breast height (1.3 m above ground; DBH) in each plot, I recorded tree species, DBH, general health (e.g., presence of boring insects), and decay class. Beetle abundance was determined by the number of decay class 2 lodgepole pine trees ha⁻¹ showing evidence of bark boring insects (the presence of outflows of dried resin on the outer bark, or by small entry holes, ~2mm in diameter, in the bark). I assumed that live pine with evidence of beetle infection at each site contained live beetles and represented a food source for breeding birds for one year. Since vegetation surveys were conducted annually, I estimated beetle abundance both in the late summer for each active nest when adult beetles were present (time t: adult beetle abundance), and for the year previous to each nest, when adult beetles had laid eggs that then overwintered beneath the bark and developed into beetle larvae available to breeding pairs throughout the following spring and summer (time t-1: beetle larvae abundance). I estimated the overall mean densities of beetle-infected pine trees for each year (Figure 2.2) from the total number of recent beetle-infected pine observed across all vegetation plots (0.04 ha) across all sites, divided by the total number of plots surveyed, for each year. I estimated site-level food availability (adult beetle abundance and beetle larvae abundance) from the total number of recent beetle-infected pine observed across all vegetation plots (0.04 ha) at each site for each year, divided by the total number of station vegetation plots conducted at each site. Thus, for each nest, I estimated the corresponding site-level densities of beetle-infected pine (times t and t-1, independently), averaged across all station vegetation plots conducted at each site and year. At
three sites where station vegetation data were not collected, I used the total number of nest vegetation plots from nests of all cavity-nesting species to obtain mean densities of beetle-infected pine trees.

**Statistical analyses**

I tested whether the beetle outbreak influenced nest densities, and/or the use of aspen trees as nest substrates, annually between 1995 and 2009, by examining the Pearson's product moment correlation coefficient of the paired associations between a) overall beetle-infected pine densities and the total number of nests found across all sites in each year, and b) overall beetle-infected pine densities and the total number of nests in aspen trees in each year (Fisher 1915).

I developed two independent generalized linear mixed-effects models to examine how characteristics of 1) nest trees, and 2) habitats (sites) surrounding nest trees influenced the probability that nests would be freshly excavated (=1) or not (=0). Since the availability of data for characteristics of nest trees and sites varied among nests (e.g., some nests had data for nest tree characteristics but no site-level information), the two models could not be compared without severely limiting the data set. Nest tree-level models examined the effects of distance to nearest forest edge (Edge), and decay stage for each nest tree on the probability of excavation. Site-level models examined the effects of beetle-infected pine densities (beetle abundance; at time \(t\) or at time \(t-1\)), and nuthatch and squirrel densities for each site on the probability of excavation. Beetle abundance from only either \(t\) or \(t-1\) was included in any one model, and models with beetle abundance at time \(t\) were compared to the counterpart models with beetle abundance at time \(t-1\). This allowed me to determine whether a lagged effect of adult beetle abundance (i.e., beetle larvae abundance) influenced excavation probabilities. Also, all biologically relevant secondary
interactions between predictor variables were examined. Site-level predictions using only beetle larvae abundance as a fixed effect variable are presented in tables and figures. Some nest trees were used more than once in a year and across years; therefore, nest tree identity (Tree ID) was included as a random effect to divide the error terms into tree versus measures within trees thereby partially accounting for correlations of repeated measures within trees.

I specified a binomial distribution with a logit link (i.e., a logistic model) for all excavation generalized linear mixed-effects models. I used Laplace approximation to generate maximum likelihood estimates, and penalized quasi-likelihood to generate parameter estimates for overdispersed models (i.e., residual scaled deviance was not equal the residual degrees of freedom), using the functions lmer in the package lme4 and glmmPQL in the library MASS, in the program R version 2.12.1 (Bolker et al. 2009, Crawley 2007, R Development Core Team 2010). To determine whether parameter estimates for fixed effects were significant in each model, I used Wald’s t-tests (Bolker et al., 2009).

In logistic regression models, the coefficients are natural logs of the odds ratios (Kleinbaum et al. 1998). Thus, I used the parameter estimates of the models to determine how the odds of a cavity being freshly excavated changed with levels in fixed effects given all other fixed and random effects in the model, using the following equations:

a) Main effects: $e^{\beta_j}$

b) Interaction effects: $e^{\beta_{x_ix_j}x_ix_j}$

Where $\beta_j =$ The parameter estimate for fixed-effect variable, $x_j$, and $\beta_{x_ix_j} =$ the parameter estimate for the interaction between the fixed-effect variables, $x_i$ and $x_j$, $i \neq j$
Results

I found a total of 418 nests over the 15-year period. Across all sites, the total number of nests found increased with mean densities of beetle-infected pine trees from 1995-2006 ($r=0.88$, $t_{10}=5.75$, $p < 0.01$; Figure 2.2), but the relationship was weak after 2006 ($r=0.48$, $t_{13}=2.00$, $p=0.07$). Across all years, 386 nests (92%) were in trembling aspen trees, and only 9 nests (2%) were in lodgepole pine and 23 (6%) in other species, including during and after the beetle outbreak. The greatest number of nests found (52), and the greatest number of aspen trees used (51) were in 2004, the year of the highest beetle-infected pine densities.

I determined whether a cavity was freshly excavated in the same season of nesting at 266 nests, 121 (45%) of which were freshly excavated, and 145 (55%) were existing cavities excavated in a year prior to nesting or non-excavated (formed only by decay processes). Each year, the proportion of freshly excavated nests ranged from 17% of all cavities used in 2009 to 70% in 2002.

The only tree-level variable to influence variation in the probability of excavation was the distance from the nest tree to the nearest forest edge. At forest edges, a greater proportion of nests were in old cavities compared to fresh cavities (Figure 2.3), and the odds that a nest was freshly excavated was $1.01 (e^{0.0053})$ times higher with each 1m increase in its location from the forest edge (Table 2.1). At the site-level, I found a significant interaction ($p=0.034$) between densities of nuthatches and beetle-infected pine: Nuthatches were 148 times ($e^{(5.00x1x1)}$) more likely to excavate a new cavity rather than use an old cavity with each increase in per ha densities of nuthatch (1 individual ha$^{-1}$) and beetle-infected pine (1 tree ha$^{-1}$; Figure 2.4).
Discussion

Overall, I found that the beetle outbreak resulted in a higher probability of excavation for nuthatches, and that despite a lower supply of aspen in the forest interior (K. Martin unpubl. data), nuthatches still showed overwhelming preference for aspen as their nest tree. My observation that the number of nests correlated positively with beetle-infected pine densities corroborates earlier findings that nuthatch population densities increased with bark beetle abundance (Figure 2.2; Norris and Martin 2010). My results that the greatest numbers of nests were in aspen in outbreak years, and the use of decayed pine snags did not increase in later years indicate that the demand for aspen as nest trees was high during and after the beetle outbreak. These results support the hypothesis that resource pulses lead to limitation of a secondary resource (Ostfeld and Keesing 2000).

Aspen as a critical resource

My result that aspen was the preferred nest tree species each year supports the finding that aspen is an integral resource in temperate forest nest webs (Figure 2.2; Martin and Eadie 1999). Yet, elsewhere in British Columbia, the greatest proportion of nuthatch nests were in decayed Douglas-fir trees (Steeger and Dulisse 2002), suggesting that other tree species can be used if sufficiently decayed to provide a soft substrate for excavation by the weak excavator (Ghalambor and Martin 1999, Steeger and Hitchcock 1998, Martin et al. 2004). In my study, almost all lodgepole pine trees were dead and in various states of decay by 2005 (Edworthy et al. 2011), but I did not observe an increase in the number of pine used for nesting. This was likely because nuthatches excavated more frequently when beetle abundance was high (Figure 2.4), and pine was still alive and not yet soft enough for excavation by the weak excavator. My observation that
only 17% of nests were freshly excavated in 2009 suggests that after the outbreak subsided and food availability declined, individuals returned to the aspen-leading forest edges where cavity availability was high and excavation was not required even though by this time pine may have been soft enough for excavation. Thus, even though nuthatches often show strong preference for decayed trees for excavation, the beetle outbreak did not result in an increase in nest substrate availability. Instead, nuthatches chose aspen trees for the duration of the study, resulting in an increased demand for aspen during high population densities, particularly in areas of high beetle-infected pine densities. The high preference of red-breasted nuthatch for aspen as the nesting tree is consistent with all other cavity-nesting vertebrates in my study, with the exception of the black-backed woodpecker (Picoides arcticus; Martin et al. 2004).

**High excavation in beetle-infected, forest interior**

Other work on the distribution of cavities across forest types at my study area showed that cavity availability increased with increasing proximity to forest edges (Aitken and Martin 2007). As a result, nuthatches were able to use a greater proportion of old nests at forest edges (Figure 2.3). However, as nuthatches shifted nest-patch locations from areas of high aspen availability, to those of high beetle-infected pine availability during the beetle outbreak, nest trees selected were farther from the edge into the conifer-dominated forest interior (Norris and Martin 2008). As there were fewer aspen trees available in the forest interior (Aitken and Martin 2007), my result that the odds of excavation increased with distance to forest edge, suggests that nuthatches were limited by the availability of old cavities in these novel habitats (Figure 2.3).

Given that clutches of nuthatches can be earlier and larger in old cavities (Wiebe et al. 2007), I postulated that nuthatches could nest in older cavities to accrue benefits of increased
fecundity in areas of high beetle abundance. Even though nuthatches tracked increases in
densities of a heterospecific cavity excavator, and used more old cavities at sites previously
occupied by downy woodpecker (*Picoides pubescens*; Norris and Martin 2010), there were
probably insufficient nesting cavities available for the burgeoning nuthatch populations at sites
and in years with high beetle abundance. As population densities increased, intra-specific
competition for cavities likely increased, and as occupancy of cavity-poor but beetle abundant
patches increased, excavation rates increased (Figure 2.4).

The increased odds of excavation with increases in densities of nuthatches and beetle
larvae indicates that a) food availability was high at newly excavated nests, and b) competition
for old cavities increased with competitor densities and food availability (Figure 2.4). Thus,
increased need to excavate was an indirect consequence of nesting in beetle abundant patches, or
viewed alternately, the ability of nuthatch to switch to mostly excavation to acquire a nest cavity
enabled them to switch to a food-rich patch. The increase in food supply early in the breeding
season may have provided nuthatches with increased energy stores to facilitate excavation
(Wiebe et al. 2006). Although nuthatches did not use more existing cavities, which may have
enabled them to initiate nests earlier and have larger clutches (Wiebe et al. 2007), the high food
supply allowed them to lay larger late clutches despite the need to excavate (Chapter 3).

The nest predation hypothesis could also explain the high excavation rates in the forest
interior. Given that new cavities often experience lower nest predation rates (Martin 1993), the
decision to excavate may have been influenced by increased nest predation risk from the forest
interior specialist, red squirrel, in these areas. The result that site-level squirrel densities did not
contribute to any variation in the excavation models may not be enough evidence to reject the
nest predation hypothesis. It is possible that: 1) individuals perceived the forest interior as an area
of higher nest predation risk, based on habitat-related cues rather than predator densities (Chalfoun and Martin 2009); 2) squirrels switched from foraging on bird nests to beetle larvae during the outbreak and high squirrel densities did not infer high nest predation risk (Mahon and Martin 2006); or 3) nuthatches assessed the densities of other nest predators, besides red squirrels, in determining whether to excavate. Nonetheless, I found little evidence to support the nest predation hypothesis, and I suspect that increased nest site constraints likely outweighed increased nest predation risk as the most important factor influencing excavation rates in beetle-infected areas.
Table 2.1. Parameter estimates for fixed effects using penalized quasi-likelihood and the logit link function, in the generalized linear mixed-effects models describing variation in excavation probabilities of red-breasted nuthatches, in central British Columbia, from 1995-2009. The models for the tree and site-level characteristics were: \( P(\text{excavated}) \sim \text{Distance to edge} \) (Edge) + Decay stage (Decay), and \( P(\text{excavated}) \sim \text{Beetle}_{t-1} \) (B) + Nuthatch density (N) + Squirrel density + B × N, respectively, with nest tree identity included as a random effect in both models. Fixed effects significantly affected the probability of excavation given all other fixed and random effects in the model where \( p<0.05 \), in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed effect</th>
<th>Parameter estimate</th>
<th>Standard error</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree-level</td>
<td>(Intercept)</td>
<td>-0.41</td>
<td>0.43</td>
<td>200</td>
<td>-0.96</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Decay</td>
<td>0.012</td>
<td>0.12</td>
<td>75</td>
<td>0.10</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td><strong>Edge</strong></td>
<td>0.0053</td>
<td>0.0023</td>
<td>75</td>
<td>2.30</td>
<td><strong>0.025</strong></td>
</tr>
<tr>
<td>Site-level</td>
<td>(Intercept)</td>
<td>0.044</td>
<td>0.28</td>
<td>190</td>
<td>0.16</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>Beetle, t-1 (B)</td>
<td>0.14</td>
<td>0.24</td>
<td>70</td>
<td>0.59</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td><strong>Nuthatch density (N)</strong></td>
<td>-2.40</td>
<td>1.10</td>
<td>70</td>
<td>-2.30</td>
<td><strong>0.024</strong></td>
</tr>
<tr>
<td></td>
<td>Squirrel (S)</td>
<td>-0.52</td>
<td>0.92</td>
<td>70</td>
<td>-0.57</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td><strong>B*N interaction</strong></td>
<td>5.00</td>
<td>2.30</td>
<td>70</td>
<td>2.20</td>
<td><strong>0.034</strong></td>
</tr>
</tbody>
</table>
Figure 2.1. Potential pathways outlining the effects of a food pulse (dashed lines) on factors influencing a decision to excavate a new nest cavity for a facultative excavating species. The nest site limitation hypothesis predicts that individuals should use old cavities in lieu of excavation in habitats with high cavity availability, low competition for cavities, and low nest predation risk (Wiebe et al. 2006). This will reduce the time required to construct a nest cavity early in the breeding season, and allow for earlier clutch initiation, and hence larger clutches. The nest predation hypothesis predicts that predators are more familiar with old cavities, thus when predator densities are high, excavation should be favoured (Martin 1995). If the food pulse provides increased energy early in the breeding season, more energy may be allocated to excavation.
Figure 2.2. Total number of red-breasted nuthatch nests found in various tree species, and site-level densities of live lodgepole pine trees with evidence of beetles (Mountain pine beetle) measured at evenly spaced 11.3-metre radius vegetation plots, across 30 mixed deciduous-coniferous forest sites, in interior British Columbia during 1995-2009.
Figure 2.3. Number of nuthatch nests that were found in cavities excavated in a year prior to nesting (Old cavity) or in the year of nesting (New cavity), in forests closer to a grassland opening, a clearcut, or a lake (<15m to edge) or farther (>15m to edge), in interior British Columbia, from 1995-2009.
Figure 2.4. Probability that nests were freshly excavated in the same season as the nesting attempt (p=1) or not (p=0), across sites with beetle larvae abundances above the mean 20 infected trees ha$^{-1}$ (high beetle; Δ) and below the mean (low beetle; ○), across nuthatch densities, at 30 sites in central British Columbia, during 1995-2009. Lines were generated from the generalized linear mixed-effects model, $P$(excavated) $\sim$ Nuthatch density (N) + Beetle$_{t-1}$ (B) + N*B, with nest tree identity included as a random effect.
Chapter 3. An insect outbreak reduces the costs of nest cavity production and increases reproductive output for an insectivore and facultative excavator red-breasted nuthatch *Sitta canadensis*

Food limitation is often found to be the primary factor influencing breeding phenology, clutch size, and nest success in birds (Lack 1947, 1954, Newton 1998). In temperate climates where breeding seasons are limited to only a few months annually, insectivores lay as many eggs as they expect to be able to feed, and the peak in nestling requirements often coincides with the peak of insect emergence (Lack 1954, Newton 1998). Nestlings that hatch earlier are able to accumulate more mass and gain more experience foraging and avoiding predators before the winter when mortality is highest (Martin 1987). Increases in food supply may advance reproduction leading to increased clutch size, number of fledglings, propensity to lay a second clutch, and the probability of natal recruitment (Arcese and Smith 1988, Martin et al. 1989, Stuart Simons and Martin 1990). Also, as adults spend less time foraging and more time defending nests, nest vigilance, and subsequently, nest survival can increase with food availability (Lack 1947, Martin 1993). However, if food pulses are shared with nest predators, increases in predator populations can suppress prey reproduction regardless of superabundant food supply (Schmidt and Ostfeld 2008). Thus, community-wide pulses in food can influence the fecundity of consumers both directly through reproductive output and indirectly through changes in nest predation risk.

For cavity-nesting species that compete for limited nesting resources with predators, food pulses that lead to increased population densities of cavity consumers and nest predators can result in increases in both competition for cavities and nest predation risk (Lack 1947, Martin 1993, 1995, Ostfeld and Keesing 2000, Aitken and Martin 2012). Species capable of excavating
their own cavities may avoid competition for cavities and exploit novel habitats but clutch size and earlier breeding may be constrained by the energy required to excavate a cavity early in the breeding season (Martin 1995). Edworthy et al. (2011) found that a food pulse led to increased breeding densities but not fecundity in obligate excavators (woodpeckers). Facultative excavators may use old cavities, in lieu of excavation, allocating the energy required to excavate cavities to breeding effort instead, and lay earlier, larger clutches during food pulses (Martin 1993, Mönkkönen and Martin 2000, Wiebe et al. 2007). However, increased nest predation risk is often associated with old cavities, imposing a potential trade-off between clutch size and nest success (Martin 1995). Thus, facultative excavators may use either old cavities to maximize reproductive output or new cavities to avoid competition and minimize nest predation in response to food pulses shared with predators. There has been little examination of the multiple factors of food and nest site availability and nest predation risk influencing the breeding strategies within facultative excavator species.

Red-breasted nuthatch (*Sitta canadensis*), hereafter nuthatch, is a facultative excavator and bark gleaner, and one of the most common insectivores and consumers of bark beetles (*Scolytinae*) in North American forests (Ghalambor and Martin 1999). Beetles (Coleoptera) comprise the major proportion of their diet during the breeding season, and nuthatches can increase their consumption of outbreak-insects, and respond positively to food pulses at the population level (Ghalambor and Martin 1999). However, nest predators may also respond positively to insect outbreaks, as insects may comprise up to 60% of the diet of squirrels and chipmunks (cavity nesters and common nest predators for nuthatch) during outbreaks (Tevis 1953, Ghalambor and Martin 1999). In the presence of adult predators, nuthatches increased the duration between nest visits and aborted more nest visits, suggesting that predator presence leads
to nest failure (Ghalambor and Martin 2000). To minimize nest predation risk and increase fecundity, nuthatch can exhibit plasticity in cavity excavation in response to increases in food supply and nest predator densities (Chapter 2). Thus, an outbreak of bark beetles may lead to earlier breeding, larger clutches, increased production of young, and multiple breeding attempts. Second broods have been documented only once in wild populations, and little research has examined how the fecundity of nuthatch changes with outbreaks in abundance of bark beetles (Ghalambor and Martin 1999).

In temperate forests, periodic large-scale insect outbreaks can result in food pulses for insectivores (Morse 1971, Dickson et al. 1979). Mountain pine beetles (Dendroctonus ponderosae) lay eggs beneath the bark of lodgepole pine (Pinus contorta var. latifolia) in late summer, and larvae reach their maximum size during the following spring before emerging as adults in late summer in British Columbia (Reid 1962). During outbreak conditions, trees overwhelmed with mountain pine beetles die as a result of infection by blue stain fungus (Grosmannia clavigera), and are then rendered unsuitable substrates for further attack, and beetle populations subside (Geiszler et al. 1980). Thus, over winter and during summer in outbreak years, mountain pine beetle larvae provide an energy-rich food source for bark insectivores capable of bark-scaling activities, but the food source is ephemeral. In this chapter, I examine how a pulse of mountain pine beetle influences the fecundity of the bark insectivore, and facultative excavator, red-breasted nuthatch.

In my study, I observed a large-scale pulse of mountain pine beetles correlated with population irruptions of red-breasted nuthatch, and increases in population densities of red squirrel (Tamiasciurus hudsonicus; Norris and Martin 2010). During the beetle outbreak, nuthatches shifted nest-patch selection away from areas of high nest site availability in trembling
aspen (*Populus tremuloides*) trees, to those of high beetle availability in beetle-infected lodgepole pine trees (Norris and Martin 2008). As a result of depleted cavity availability in these patches, nuthatches excavated more frequently than using old cavities (Chapter 2). Immediately following the insect outbreak, nuthatch population densities crashed, suggesting a negative consequence associated with the food pulse. Thus, despite the increased use of new cavities, which are reportedly safer from predation, increased nest predator densities may have suppressed reproduction as a result of higher predator-prey encounter rates (Schmidt and Ostfeld 2008, Chalfoun and Martin 2009). In this chapter, I examine the reproductive mechanisms underlying the correlations among population densities of nuthatches and squirrels, beetle abundance, and cavity reuse, specifically how the beetle outbreak influenced reproductive output and nest success. If food supply limits breeding phenology, clutch size, and/or the ability to avoid nest predation, then the food pulse may lead to higher fecundity, but the increased propensity to excavate cavities and higher predator densities may constrain reproductive output and nest success, respectively. Thus, I examine the nature of the direct and indirect effects of fluctuating food resources on prey and their predators that might result in consumers facing a trade off in nest predation risk.

**Methods**

Fieldwork was conducted within the warm and dry Interior Douglas-fir biogeoclimatic zone of central British Columbia, Canada (Meidinger and Pojar 1991). The area comprises mixed coniferous-deciduous forest, with trembling aspen, Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), lodgepole pine, and hybrid white and Englemann spruce (*Picea glauca x engelmannii*) as the predominant tree species. Seventeen of the 30 study sites were located near Riske Creek,
40 km west of the City of Williams Lake, and 13 sites were near Knife Creek, 20-40 km east of Williams Lake (52°14’N, 122°12’W). Sampling sites (mostly 15 to 32 ha in size) varied in composition from continuous forest to five sites that were a series of ‘forest groves’ (0.2 to 5 ha) within a grassland matrix. Additional study area details are given in Martin and Eadie (1999) and Aitken et al. (2002).

**Nest monitoring**

Field data were collected from May through July at 30 sites, during 15 years, 1995-2009. I conducted systematic nest searches, point count surveys, and vegetation surveys to monitor breeding activity, abundance, and habitat associations of all cavity-nesting species. I found nests by visually inspecting previously occupied cavities and by following and observing breeding behaviours of adults and pairs at all sites. I used a video camera cavity monitoring system (starting in 2005; I could reach nests with a maximum height of 15 m from the ground), or a mirror and halogen flashlight from the ground or a ladder (reaching nests with a maximum height of 6 m), to inspect cavities and monitor a total of 420 red-breasted nuthatch nests in natural cavities (formed by excavators or decay), approximately every 4-7 days.

Nests were considered active by the presence of eggs, or chicks. To assess measures of fecundity, I recorded date of first egg laid, clutch size, incubation period, hatch date of first nestling, the number of nestlings hatched, the number of young to fledge, fledging date of first nestling, and nest fate (failed or fledged at least one nestling). To determine the date of first egg laid at nests where it was not directly observed (where one egg was found in an active nest, followed by more eggs in subsequent days), I assumed that one egg was laid per day and counted backwards from the final egg laid, at nests found during laying before the clutch was complete.
To determine clutch size, I counted the total (maximum) number of eggs observed in a nest while adults were incubating. To avoid using estimates of incomplete clutches, I used data for which I observed the same total number of eggs at least twice. Nuthatches begin incubation on the day that the last egg was laid; therefore, the incubation period was calculated as the number of days beginning at the date of the last egg laid and ending at the hatch date (Ghalambor and Martin 1999). Hatch date was a more accurate measure of breeding phenology than date of first egg laid because nuthatches often buried their eggs beneath nest material while laying, which impeded my ability to accurately count eggs during the laying phase. I determined hatch date as the first day I observed at least one chick hatching, or I estimated from chick age if all chicks hatched were < 4 days old and the observer could be confident of chick age. Chick age was determined by the presence of eggshells in the nest (parents remove eggshells within 1-2 d of hatching), capability of chicks to lift their heads (heads lift ~ 2 d post-hatch), colour of the skin (pink indicates a chick < 4 d), the presence of down or pin-feathers (down indicates a chick between 3-7 d, pin feathers indicate a chick > 7 d), whether the eyes were closed or open (eyes open ~ 4 d). Nests were determined successful (survived) if at least one chick was observed to fledge, or was in the nest at least 14 days after hatching, the minimum number of days required for nuthatch nestlings (Ghalambor and Martin 1999). I assumed nests failed where eggs disappeared during incubation, chicks were dead in the cavity, or the cavity was empty before 14 days post hatch. I noted any sign of predation (predator usurped cavity, cavity was torn open, or woodchips were found on the nest material which indicated that the cavity was enlarged by a predator, typically a red squirrel which is much larger in body size than nuthatch thus will chew the entrance to gain access to smaller cavities). Where possible, I used mist nets and other nets to cover the nest entrance to capture and colour-band individual adults on breeding territories. This allowed me to determine
cases of multiple breeding attempts within and across seasons. I noted the cavity type as freshly excavated in the same year as breeding (where I observed an adult excavating earlier in the breeding season, or fresh woodchips below the cavity entrance or at base of the nest tree) or not (formed in a previous year; where I monitored the cavity in a previous year, or the cavity entrance appeared worn). Since many nests were difficult to access with a ladder prior to the year that I obtained cavity-monitoring video cameras in 2005, the type of data collected varied across nests. For example, there were more nests with data that could be easily collected from the ground (e.g., whether the cavity was freshly excavated or not) compared to nests that required multiple observations of the inside of the nest cavity during critical nesting periods (e.g., clutch size). As a result, the sample sizes of nests with adequate fecundity measures were imbalanced across variables. Nonetheless, I am confident that the fecundity data collected were representative of the whole population examined.

**Beetle abundance**

During the study period, an outbreak of mountain pine beetles progressed over all sites, with incidence of beetle attacks on pines increasing sharply after 2002 (Drever et al. 2009). By 2005, over 95% of the mature lodgepole pine trees (40% of the trees on the sites) were dead (Edworthy et al. 2011). To determine habitat associations of nests, 0.04-ha circular vegetation plots were established and centered at each active nest and point count station (one plot ha⁻¹) during 1995-2009. For all trees ≥12.5 cm diameter at breast height (DBH; outside bark diameter measured at 1.3 m above ground) in each plot, I recorded tree species, DBH, general health (e.g., presence of boring insects), and decay class. Decay class 1 was a live, healthy tree, 2 a live tree with visible sign of bark boring insects, and 3-8 were standing dead trees in progressive states of decay.
Beetle abundance was determined by the number of decay class 2 lodgepole pine trees ha$^{-1}$ showing evidence of bark boring insects (the presence of outflows of dried resin on the outer bark, or by small entry holes, ~2mm in diameter, in the bark). I assumed that these live pine trees with evidence of beetle infection contained live beetles and represented a food source for breeding birds at each site for one year. Since vegetation surveys were conducted annually after nests were finished, I estimated beetle abundance both in the late summer for each active nest when adult beetles were present (time $t$: adult beetle abundance), and at the site in the year previous to each nest (time $t-1$), when adult beetles had already laid eggs that then overwintered beneath the bark and developed into beetle larvae available to breeding pairs throughout the following spring and summer of time $t$ (time $t-1$: beetle larvae abundance). I estimated food availability (adult beetle abundance and beetle larvae abundance) from the total number of recent beetle-infected pine expressed on a per ha basis divided by the total number of 0.04 ha vegetation plots for each site and year. At three sites where station vegetation data were not collected, I used the total number of nest vegetation plots from nests of all cavity-nesting species to obtain mean densities of beetle-infected pine trees. Even though the beetle outbreak occurred primarily in 2003 and 2004 (Norris and Martin 2010), I observed substantial spatiotemporal variation in the distribution of beetle abundance (Figure 3.1). Thus for each nest, I assigned site-level densities of beetle-infected pine detected in same year as the nest (time $t$: adult beetle abundance) and in one year prior to the nest (time $t-1$: beetle larvae abundance). I predicted that adult beetle abundance later in the breeding season should be important to fecundity for fledgling survival, whereas beetle larvae abundance throughout the breeding season should improve nestling survival.
Nuthatch and squirrel population densities

Point count surveys were conducted to estimate population densities of red-breasted nuthatches and red squirrels at 27 sites, during 1995-2009. In continuous forest sites, point count stations were spaced evenly in a 100 x 100 m grid starting at a grassland or wetland edge and extending into the forest (one plot ha⁻¹). In forest groves where trees were patchily distributed, I placed point count stations at least 100 m apart. From 0500-0930 hours, I recorded the species, and number of individual birds and squirrels detected within 50-m radius 6-minute point counts at each station (mostly 15-32 point count stations site⁻¹). I surveyed 425 stations across 27 sites three times (rounds) each year. The three additional sites were not surveyed using point counts, but were used for nest and vegetation monitoring. Further details of population monitoring methods are provided in Martin and Eadie (1999) and Drever et al. (2008). I did not consider observations at multiple point count stations within sites to be statistically independent of one another; therefore I summed the total number of individuals detected at all point counts across all rounds within sites to produce site totals in each year by species. To obtain densities estimates for nuthatches and squirrels, I divided the site totals by the total number of counts and rounds conducted for each site and year. Thus for each nest, I assigned site-level densities of nuthatches and squirrels (mean individuals ha⁻¹) to the site and year in which the nest was found.

Statistical analyses

Four groups of mixed-effects models were constructed with the response variables expressed on a per nest level, namely: number of eggs laid (clutch size), number of chicks hatched, number of chicks fledged, and whether the nest fledged at least one nestling or not (nest survival). The fixed effects for possible inclusion in these models were: beetle abundance per ha (at each site for the
current (time t) and previous (time t-1) years of the active nest), Julian hatch day, clutch size, whether the cavity was freshly excavated or old (excavated in a previous year), nuthatch density per ha, and squirrel density per ha. Initially, the number of visits by observers was included as a possible fixed effect, but this was not significant for any of the models and is not further discussed in this paper. Since hatch day showed substantial annual variation (Figure 3.2), which may be due to factors unrelated to beetle abundance, I transformed the variable, Julian hatch day, by taking the absolute value of the difference between the annual mean hatch day and the observed hatch day for each nest.

As some nest trees were used more than once across years, nest tree identity was included in all models as a random effect to account for the hierarchical error structure representing nest trees. Further, multiple nests (in different trees) occurred within sites; therefore, site was also included as a random effect in all models. To determine whether adult beetle or beetle larvae abundance was more important in influencing fecundity and/or nest success, all fixed and random effects were held constant and fully-parameterized models with beetle abundance at time t were compared to the counterpart models with beetle abundance at time t-1. For each response variable, I selected the model that explained the greatest proportion of variation, and in all cases beetle larvae abundance explained more variation than adult beetle abundance. All biologically relevant secondary interactions between predictor variables were examined.

I used a generalized linear mixed model (Crawley 2007) and specified a Poisson distribution for clutch size, number of chicks hatched, and number of fledglings as the response variables, and a binomial distribution for nest survival (fledged=1, failed=0). For models using the Poisson distribution the default log link was used, whereas the default logit link was used for models with the binomial distribution. Since nests found at different nesting stages can bias nest
success estimates (Mayfield 1975), I applied a logistic-exposure adjustment to binomial
distribution in nest survival models, which weights each observation based on the inverse of the
number of days that the nest was observed, thus providing estimates for nest survival without
assuming when nest loss occurs (Shaffer 2004). For all models, the hierarchical errors were
assumed to have normal distributions. Due to the hierarchical error structure of the observational
data, penalized quasi-likelihood was used to calculate parameter estimates and standard errors
(Bolker et al. 2009). As likelihood ratio tests cannot be used on quasi-likelihood estimates in
traditional model selection techniques, I used Wald’s t-tests to progressively eliminate fixed
effects that did not significantly account for variation in the response variables, given all other
fixed and random effects in the models (Crawley 2007, Bolker et al. 2009). All data analyses
were conducted using Penalized quasi-likelihood estimates were obtained using the functions
glmmPQL in the library MASS, and logexp for binomial models in the program R version 2.12.1
(Shaffer 2004, Bolker et al. 2009, R Development Core Team 2010).

In log-link Poisson regression models, the coefficients are inverse natural logs of the
linear predictor values (Kleinbaum et al. 1998, Crawley 2007). Thus, I used the parameter
estimates of the final models to determine how clutch size and the number of fledglings was
predicted to change with levels in fixed effects given all other fixed and random effects in the
model, using the following equations:

a) Main effects: $\ln(\beta_j)$

b) Interaction effects: $\ln(\beta_{x_i,x_j} \times x_i x_j)$

Where $\beta_j = \text{The parameter estimate for fixed effect, } x_j, \text{ and } \beta_{x_i,x_j} = \text{the parameter estimate for the interaction between the fixed-effect variables, } x_i \text{ and } x_j, i \neq j.$
Results

Beetle abundance showed variation across sites and years with the greatest increases at the site-level occurring during 2003 and 2004 (Figure 3.1). Nuthatch fecundity showed significant annual variation in clutch size, hatching day, number of fledglings, and the percent of nests to successfully fledge at least one young (Figure 3.2). Mean clutch size varied between 5.3 eggs ± 0.63 standard error (SE) in 2005 and 6.5 eggs ± 0.71 SE in 2001, with an overall mean of 6.0 eggs ± 0.11 SE. Hatch day ranged between 6 June (Julian Hatch day 157 ± 8.22 SE) in 2000 and 1 July (Julian hatch day 182 ± 3.49 SE) in 2002, with an overall mean of 21 Jun (172 ±1.31 SE). Of nests that fledged at least one young (successful nests), the mean number of nestlings to fledge varied between 3.6 fledglings ± 0.48 SE in 2000 and 5.7 fledglings ± 0.25 in 2009 with an overall mean of 5.1 ± 0.11 SE. The percent of successful nests varied between 70% in 2003 and 100% in 2001, 2006 and 2007.

Phenology and reproductive output

For clutch size models, I found a significant interaction between hatch day and abundance of beetle larvae (Table 3.1). At sites and in years with low beetle larvae abundance, I observed the usual seasonal relationship in birds whereby the number of eggs laid declined as clutches were laid later in the breeding season, with a mean decline of 1 egg for each 20 days later the clutch was laid; however, at sites and in years with high beetle larvae abundance, mean clutch size (~6 eggs) remained relatively constant throughout the season (Figure 3.3). I confirmed seven nests to be second broods of six colour-marked pairs that fledged one successful brood already in the season, and one pair that failed in their previous nesting attempt. All seven cases occurred in 2003, 2005 and 2007, during and immediately after the peak of beetle larvae abundance. In nests
that fledged at least one young, the number of fledglings were predicted to increase by three for each increase in the number of beetle-infected pine trees per plot, and by one fledgling for each increase in one nuthatch detected per point count. However, there was a predicted decrease by one fledgling for each increase in one squirrel detected per count.

Nest survival
I found 197 nests for which I could accurately assess nest survival, 165 of which were successful (at least one chick fledged or chicks in the nest were aged at least 14 days old), and 32 failed (nest was empty before chicks hatched or before chicks were 14 days old, or chicks in the nest were dead). Of the 32 failed nests, I found evidence for predation at 20 nests (predator usurped cavity, cavity was torn open, or woodchips were found on the nest material which indicated that a larger species, such as a red squirrel, chewed the cavity entrance to gain access to the cavity).

I found no significant fixed-effects variables for the number of chicks hatched nor for nest survival. For best-fit models of clutch size and number of fledglings, I found no effect of cavity freshness (whether the cavity was excavated in the same year or in a year prior to nesting; Table 3.1).

Discussion
Overall, I found strong support for the hypothesis that food limits fecundity, weak evidence to suggest that nest predation risk influences reproductive output, and no indication that excavation (or reuse of old cavities) incurs a cost to fecundity. My two main findings were that: 1) later clutches were larger at sites and years with high beetle larvae abundance, and 2) the number of nuthatch fledglings per successful nest increased with increasing beetle larvae abundance and
nuthatch densities, but declined with squirrel densities. I suspect that high spatiotemporal variation in fecundity and beetle abundance inhibited my ability to detect an overall increase in fecundity in outbreak years (Figures 3.1, 3.2).

**Phenology and reproductive output**

Earlier nests of insectivores are often larger and have a higher probability of survival than later nests because insect emergence peaks once early in the season, providing maximal food during the peak of nestling energy requirements (Perrins 1965, Grant et al. 2005). My result that later hatching nests were larger when surrounded by high site-level abundance of beetle larvae suggests that adults did not adjust their clutch size according to nesting phenology during the beetle outbreak. Similarly, Eurasian nuthatches (*Sitta europaea*) showed a decline in clutch size with hatch date, but laid larger clutches in years with later breeding (Pravosudov 1993). When food was supplemented throughout the breeding season for a population of song sparrows (*Melospiza melodia*) in British Columbia, pairs raised larger and later nests and had multiple breeding attempts per season (Arcese and Smith 1988). Mountain pine beetle larvae and pupae were available from late summer after beetle eggs hatched, until the following late summer, when adult beetles emerged (Reid 1962). Thus, during the outbreak, food was available to residents throughout the breeding season, rather than during a single peak. I confirmed only seven nests as second clutches during and after the peak of beetle larvae abundance, but there were likely more because many adults were unmarked. Thus I suggest that the beetle outbreak extended the period of food availability during the breeding season, which allowed nuthatches to lay larger clutches and feed more nestlings later in the season, have multiple breeding attempts, and fledge more young per nest during the energetically costly nestling feeding stage.
My findings that reproductive output increased at sites and in years with high beetle larvae abundance may explain why nuthatches shifted nest site preferences from areas of high availability of aspen (important for nest sites) to those of high availability of beetle-infected pine, during the outbreak (Norris and Martin 2008). In Eurasian nuthatches, annual production of young increased with food abundance, but was negatively density dependent, particularly at territories that were used only during high population densities (Nilsson 1987). Yet food supplementation advanced laying dates at lower quality territories in blue tits (Parus caeruleus; Svensson and Nilsson 1995). In my study, nuthatch population densities were highest during 2003 and 2004, the greatest outbreak years (Norris and Martin 2010), and many pairs likely settled at previously unoccupied territories in beetle-abundant areas during this time. In other work, I showed that nuthatch exhibited positive density-dependent population growth with increases in nest availability from another small-bodied cavity excavator, downy woodpecker (Norris and Martin 2010). Thus my result that the number of fledglings increased with beetle larvae abundance and nuthatch densities indicates that the beetle outbreak increased territory quality and led to positive density-dependent reproductive output at previously unoccupied territories.

Later and smaller clutches, but higher nest survival of pairs in freshly excavated cavities is often cited as evidence that excavation imposes a trade-off between reproductive output and nest success (Martin 1995, Wiebe et al. 2007). Yet, I found no evidence that fresh and old cavities varied with respect to phenology, reproductive output, or nest survival. I suspect that beetle larvae abundance may have dissipated any existing relationship between fecundity and cavity freshness for nuthatch (Wiebe et al. 2007). The increased need to excavate was an indirect consequence of nesting in beetle abundant patches, but the increase in food supply early in the
breeding season may have provided nuthatches with the energy required to excavate. My result that clutches were not smaller later in the season and were laid no later at beetle-abundant sites suggests that the major costs associated with excavation, delayed breeding and smaller clutches were alleviated with high food availability. But the result that fresh cavities were no safer from predation suggests that nest predation risk may have increased at beetle-rich sites.

Nest survival

As 63% of the failed nests were confirmed predated I suggest that predation was the major cause of nest loss for nuthatches. Nest predation rates can increase with increased predator-prey encounter rates when densities of predators and prey increase and/or the occupancy of nest sites accessible to predators increases (Chalfoun and Martin 2009, 2010). In red-breasted nuthatches, predator presence reduces nest success as a result of parents reducing the frequency and duration of nestling feeding visits (Ghalambor and Martin 2000). Higher predator-prey encounter rates may have arisen during both high nuthatch densities and high beetle abundance because breeding densities and squirrel densities co-varied positively during the beetle outbreak (Norris and Martin 2010) and lower nest-tree availability in beetle abundant areas means higher cavity occupancy rates (Norris and Martin 2008). However, if predators forage on the shared food pulse instead of bird nests, then increased predator-prey encounter rates may not result in increased nest predation rates, as was shown with chestnut-backed chickadee *Poecile rufescens* (Mahon and Martin 2006). I found a negative effect of squirrel density on the number of fledglings but I found no effect of squirrel density on nest survival. Further, my finding of an overall nest survival rate of 84% is higher than other reports of nest mortality in this species (76% in Arizona; Fontaine and Martin 2006). Thus, nest predator presence may negatively affect reproductive output by disrupting
nestling care, but may not influence nest survival, particularly during a community-wide food pulse that provides an alternate food source for predators.

**Caveats and future research**

I highlight a few important caveats to my study. First, I could only confirm failure at 32 nests, thus inferences of nest survival remain speculative. The result that both beetle larvae abundance and squirrel density significantly affected the number of fledglings but did not influence nest survival may indicate either a statistical type II error as a result of the paucity in nest failure data, or that the benefits of higher reproductive output due to high beetle larvae abundance outweighed the negative effects of nest predation. Also, I lack adult survival data, and thus was unable to directly measure recruitment and dispersal. Consequently, I was unable to detect the degree to which reproduction versus migration influenced population growth and density dependent processes. Next, as in many ecological studies, my observations are correlations that may not imply causation. Many other factors that may influence the reproductive trade-offs made by nuthatches, such as age, experience, adult condition, and other environmental variables were not measured in this study (Martin 1995). Nonetheless, this is the first study to document the direct effects of resource constraints and indirect effects of conspecific and predator densities on reproductive output and nest survival in a facultative cavity excavator during a large-scale resource pulse.

A key implication of this study is that resource pulses can result in major changes to reproductive decisions that may have significant fitness outcomes. The beetle outbreak diminished the negative effects of excavation, indicating that resource pulses can influence the interaction between food- and nest site limitation of cavity nesters. The resiliency of nuthatches
to spatiotemporal variation in resource availability may explain their irruptive nature. The plasticity in resource use may allow nuthatches to respond rapidly to resource pulses. Cavity-nesting species interact within a community of competitors, facilitators, and predators (Martin and Eadie 1999). Examination of how community-wide processes change with resource pulses may further elucidate the effects of resource constraints and species interactions on fecundity.
Table 3.1. Parameter estimates for fixed effects using penalized quasi-likelihood, in the best-fit generalized linear mixed-effects models describing variation in fecundity of red-breasted nuthatches in central British Columbia, from 1995-2009. I used the log link function and the Poisson distribution for models: No. eggs laid ~ Beetle_{t-1} (B) + Hatch day (H) + B × H, No. fledged ~ Beetle_{t-1} + Nuthatch density + Squirrel density, with Tree ID and Site included as hierarchical random effects in both models. Fixed-effect variables including interactions that significantly accounted for variation in response variables at the 0.05-level of significance are in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed effect</th>
<th>Parameter estimate</th>
<th>Standard error</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
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<tr>
<td>No. eggs laid</td>
<td>(Intercept)</td>
<td>2.5</td>
<td>0.22</td>
<td>64</td>
<td>11</td>
<td>&lt;0.001</td>
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<td></td>
<td>Beetle_{t-1} (B)</td>
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<td>0.17</td>
<td>23</td>
<td>-2.6</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Hatch day (H)</td>
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<td>0.0013</td>
<td>23</td>
<td>-3.1</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>B*H interaction</td>
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<td>0.001</td>
<td>23</td>
<td>2.6</td>
<td>0.016</td>
</tr>
<tr>
<td>No. fledged</td>
<td>(Intercept)</td>
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<td>0.049</td>
<td>87</td>
<td>32</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Beetle_{t-1}</td>
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<td>0.021</td>
</tr>
<tr>
<td></td>
<td>Nuthatch density</td>
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<td>0.17</td>
<td>28</td>
<td>1.9</td>
<td>0.067</td>
</tr>
<tr>
<td></td>
<td>Squirrel density</td>
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<td>0.14</td>
<td>28</td>
<td>-1.9</td>
<td>0.064</td>
</tr>
</tbody>
</table>
Figure 3.1. Temporal and spatial variation in the mean number of beetle-infected pine per 11.3m-radius circular plot in interior British Columbia, during 1995-2009. Lines indicate independent sites ranging between 15-32 ha in size.
Figure 3.2. Summary of fecundity characteristics of Red-breasted Nuthatch nests in interior British Columbia, Canada, from 1999 (99) to 2009 (09). Error bars indicate standard errors of the mean.
Figure 3.3. Clutch sizes across various Julian hatch days for 120 red-breasted nuthatch nests, at sites and years with beetle larvae abundances above the median 15 infected trees/ha (high beetle; ●) and below the median (low beetle; ○), across nuthatch densities at 30 sites in central British Columbia, during 2000-2009. For each nest, the annual mean Julian hatch day was subtracted from the observed Julian hatch day to derive deviations. Lines are estimated using predicted values generated from the best-fit general linear mixed-effects model, No. eggs laid ~ Beetle_{t-1} + Hatch day + Beetle_{t-1}*Hatch day | Site/TreeID (see Table 3.1 for parameter estimates).
Chapter 4. The counterbalancing effects of food and nest site constraints and nest predation risk on fecundity of a secondary cavity-nesting bird

A major challenge in disturbance ecology centers on understanding the direct and indirect effects of large-scale habitat perturbations on the fecundity of individuals within communities. Lack’s (1954) hypothesis that food limits clutch size in birds such that adults lay only as many eggs as they expect to successfully rear has been widely accepted as a primary determinant of fecundity. As access to food can be limited by predation risk and nest site availability, the food limitation hypothesis has since been modified to include these factors in describing patterns in avian fecundity (Martin 1995). For example, in the presence of predators adults often limit the clutch size, clutch mass, and nestling provisioning rates at nests, but these negative effects can be reduced with a large-scale increase in food availability (Martin 1992, Fontaine and Martin 2006, Travers et al. 2010). In addition, types of nest sites (e.g., ground, tree branch, tree cavity, etc.) vary in vulnerability to nest predation risk, and when nest site and nest predation were examined across 123 species, these variables explained over 50% of the variation in clutch size and annual fecundity (Martin 1995). However, for tree cavity-nesting species that tend to experience relatively low nest predation rates, availability of nest sites and diet appear to be the most important factor limiting clutch size (Martin 1993, Wiebe et al. 2006). Although food supply, nest predation, and nest site availability interact to influence reproductive traits differently within and across species, it remains unclear how species respond to changes in these direct and indirect constraints during resource pulses.

In tree cavity-nesting communities, or nest webs, species and individuals compete, often with nest predators, for a limited number of cavities that are required for reproduction (Martin
and Eadie 1999, Aitken et al. 2002). In chapter 3 I showed that excavator species may exploit novel habitats during resource pulses, but it remains unclear how species that are unable to excavate new cavities can capitalize on resource pulses. Mountain chickadee (*Poecile gambeli*) is an obligate secondary-cavity nester, which relies on excavator species for nest site production (McCallum et al. 1999). As a result of cavity-limited reproduction, individuals may nest in suboptimal areas of high competition or high nest predation risk (Aitken and Martin 2012).

Mountain chickadee and American red squirrel (*Tamiasciurus hudsonicus*), a common predator of chickadee nests that nests and roosts in cavities, are common year-round residents in British Columbia (Aitken et al. 2002, Norris and Martin 2010). Breeding territory selection can occur throughout the winter; thus chickadees may minimize nest predation risk by choosing territories with the lowest predator densities (McCallum et al. 1999, Turcotte and Desrochers 2003). However, encounters with predators may be difficult to avoid during resource pulses that are shared with predators (Schmidt and Ostfeld 2008). Both chickadees and squirrels are opportunistic insectivores that can switch their foraging substrate depending on forest insect abundance, and respond positively to insect outbreaks (Tevis 1953, McCallum et al. 1999). In British Columbia, large-scale outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) and western spruce budworm (*Choristoneura occidentalis*) correlated with increases in densities of mountain chickadee and red squirrel (Norris and Martin 2010, Norris et al. In Review). If predator densities are high across all territories, adults may minimize the risk of nest predation at the nest site level by choosing safer cavities (Albano 1992, Wesołowski 2002), or by modifying their behaviour at the nest to reduce risk of detection by predators (Fontaine and Martin 2006). Upon failure of first broods, mountain chickadee will lay second clutches, but nests following
successful first broods have been reported only in nest-boxes and not in tree cavities (McCallum et al. 1999).

Resource pulses may indirectly lower nest predation risk if the level of risk varies across cavity characteristics and competition for safer cavities is reduced. For example, cavities with smaller entrances may restrict larger-bodied predators, such as squirrels (Wesołowski 2002), and nests higher above the ground may be safer from terrestrial predators such as snakes and rodents (Nilsson 1984, Albano 1992, Fisher and Wiebe 2006). In British Columbia, mountain chickadee uses cavities with the smallest-sized entrances among all secondary cavity nesters, which are excavated by the smallest-bodied excavators, downy woodpecker (Picoides pubescens), and red-breasted nuthatch (Sitta canadensis), and one medium-sized excavator, red-naped sapsucker (Sphyrapicus nuchalis; Aitken et al. 2002, Martin et al. 2004, Norris et al. In Review). The outbreak of mountain pine beetle led to increases in populations of the bark beetle consumers, woodpecker and nuthatch, and subsequently, the supply of smaller cavities increased (Norris and Martin 2010, Edworthy et al. 2011). During the beetle outbreak, mountain chickadee used a greater proportion of cavities excavated by downy woodpecker and nuthatch, suggesting a reduction in competition for smaller cavities (Norris et al. In Review). The fecundity consequences of this shift in cavity use during the beetle outbreak have not yet been studied.

Community-wide food pulses can increase fecundity of cavity nesters directly through food supply and indirectly through changes in resource constraints or nest predation risk (Mahon and Martin 2006, Norris and Martin 2008). In British Columbia, the outbreak of mountain pine beetle from 2003 to 2004 led to increased reproductive output by reducing the costs of cavity excavation for red-breasted nuthatch (Chapters 2, 3). In another study of a similar-sized cavity-excavator species, chestnut-backed chickadee (Poecile rufescens), nest survival increased with
pulses in seed production, when an alternate food source was available to squirrels (Mahon and Martin 2006). However, the effect of a shared food pulse on fecundity can differ across species, depending on the behavioural responses of predators, and depending on other secondary and tertiary indirect impacts (Robb et al. 2008, Schmidt and Ostfeld 2008). The direct and indirect effects of a food pulse shared with nest predators have not been examined in a secondary cavity nester.

In this chapter, I examined how fecundity of the mountain chickadee was influenced 1) directly by food supply and 2) indirectly by nest site characteristics and nest predation risk, and 3) by the interaction between food supply and nest predation risk, in British Columbia. I hypothesized that if chickadee fecundity was influenced by: 1) competition for food, then site-level densities of conspecifics, beetle-infected lodgepole pine (Pinus contorta var. latifolia) trees (mountain pine beetle), and live Douglas-fir (Pseudotsuga menziesii var. menziesii) and hybrid spruce (Picea glauca x engelmannii) trees (western spruce budworm substrates), should best describe variation in reproductive output; 2) nest predation risk, then a) nest survival should decline with increasing predator densities and in larger, predation-prone cavities, and b) the number of feeding trips, which typically increase with increasing brood size (Grundel 1987), should be limited to reduce risk of detection by predators when predator densities are high (Ghalambor and Martin 2000); and 3) an interaction between food supply and nest predation, then a) high beetle abundance should allow parents to afford greater nestling care, and b) reduction in competition for safer cavities produced by downy woodpecker and red-breasted nuthatch, as a lagged effect of the beetle outbreak, should lead to increased survival rates.
Methods

Field data were collected from May through July 1995-2009, at 30 sites within the warm and dry Interior Douglas-fir biogeoclimatic zone of central British Columbia, Canada. The area comprises mixed coniferous-deciduous forest with predominant tree species, trembling aspen (*Populus tremuloides*), Douglas-fir, lodgepole pine, and hybrid spruce (Meidinger and Pojar 1991). Seventeen of the 30 study sites were located near Riske Creek, 40 km west of Williams Lake (52°14’N, 122°12’W), and 13 sites were near Knife Creek, 20-40 km east of Williams Lake. Sampling sites ranged from 15 to 32 ha (one 7-ha site) in size, and varied in composition from continuous forest to five sites that were comprised of a series of ‘forest groves’ (0.2 to 5 ha) within a grassland matrix. Additional study area details are given in Martin and Eadie (1999) and Aitken et al. (2002). I conducted systematic nest searches, point counts, and vegetation surveys to monitor breeding activity, population densities, and habitat associations of all cavity-nesting species.

Nest monitoring

To find nests, I visually inspected previously occupied cavities, and observed breeding behaviours of adults and pairs. I used a video camera cavity monitoring system (2005-2009), or a mirror and halogen flashlight from the ground or a ladder, to inspect cavities and monitor all accessible nests in natural cavities (formed by excavators or decay), every 4-7 d. Nests were considered active by the presence of eggs or chicks. To measure fecundity, I recorded date of first egg laid, clutch size, incubation period, hatch day of first nestling, the number of nestlings hatched, the number of young fledged, date of first nestling to fledge, and nest fate (failed or fledged at least one nestling). For clutch size estimates, I counted the maximum number of eggs,
observed at least twice, for a completed clutch. Hatch day was a more accurate measure of breeding phenology than date of clutch initiation because chickadees often bury their eggs beneath nest material while laying, which impeded my ability to accurately count eggs during the laying phase. I determined hatch day as the first day I observed at least one chick hatching, or I estimated from chick age if all chicks hatched were < 4 days old and the observer was confident of chick age. Nests were determined as successful if chicks were observed to fledge, or were still in the nest at least 14 days after hatching, the minimum number of days that mountain chickadee nestlings were observed to fledge from a nest during my study. Otherwise, I assumed nests failed. I noted any sign of predation attempts (predator usurped cavity, cavity was torn open, or nest material was pulled out of the cavity). I assumed constant daily nest survival for all nests, but accounted for the number of days that the nest was observed in nest survival models (Shaffer 2004; see Statistical analyses). Upon nest completion, I measured tree and cavity characteristics, including cavity entrance area size, and the origin of the cavity formation (cavity formed by excavator or natural decay). To determine cases of multiple breeding attempts of individuals within seasons, I used mist nets, and other nets to cover the nest entrance, to capture and colour-band adults on breeding territories.

**Nestling feeding observations**

I observed the rate at which adults brought food to nestlings by counting the total number of trips made per observation period, at each nest between 2004 and 2008. Observation durations ranged from 15-40 min and were conducted between 5 am and noon. I waited ~20 min prior to conducting a feeding observation to ensure that the observation period encompassed a ‘feeding bout’ or a time that food delivery was consistent (1+ feeding trips / 5 min interval). Nestlings
were on average 7 d post-hatch at the time when feeding observations were conducted, but ranged from 2-17 d post-hatch. Since the parental effort among nests vary, the age of nestlings influences the food delivery rate, and the food delivery rate plateaus at 10 d post-hatch in mountain chickadee (Grundel 1987). I 1) removed duplicate feeding observations at nests, selecting only the observations conducted at the age closest to 10 d, and 2) included nestling age as a fixed-effect variable in models describing variation in nestling feeding rates.

**Population densities**

Point count surveys were conducted to estimate population densities of mountain chickadees and red squirrels at 27 sites, during 1995-2009. In continuous forest sites, point count stations were spaced within a 100 m square grid ≥ 50 m from a grassland or wetland edge (one station ha⁻¹). In forest groves where trees were distributed patchily, point count stations were placed at least 100 m apart. From 0500-0930 hours, I recorded the species, and number of individual birds and squirrels detected within 50-m radius 6-minute point counts at each station (7-32 stations site⁻¹). I surveyed 425 stations across 27 sites three times (rounds) each year. Three additional sites were not surveyed using point counts, but were used for nest and vegetation monitoring. Further details of population monitoring methods are provided in Martin and Eadie (1999) and Drever et al (2008). I divided the total number of individuals observed on all rounds by the total number of point counts to obtain estimates of mean individuals ha⁻¹ for each site and year.

**Vegetation surveys**

To determine habitat conditions surrounding nests, 0.04-ha circular vegetation plots were established and centered at each active nest and point count station every year during 1995-2009.
For all trees ≥12.5 cm diameter measured at 1.3 m above ground (DBH) in each plot, I recorded tree species, DBH, general health (e.g., presence of boring insects on the bole), and decay class. Decay class 1 was a live, healthy tree, 2 a live tree with visible sign of bark boring insects or heart rot fungus, and 3-8 were standing dead trees in progressive states of decay (Thomas et al. 1979). During the study period, an outbreak of mountain pine beetle occurred across all sites, with incidence of beetle attacks on pines increasing sharply after 2002, and by 2005 over 95% of the mature lodgepole pine trees (40% of the trees on the sites) were dead (Drever et al. 2009, Edworthy et al. 2011). However, the onset of the beetle outbreak showed temporal and spatial variation with respect to site level characteristics (Drever et al. 2009); therefore, I examined site-level effects of beetle abundance. In British Columbia, beetle eggs are laid beneath the bark in late summer where they then overwinter; beetle larvae complete development in the following summer before emerging as adults (Reid 1962). I determined beetle-infected pine densities per ha as the total number of decay class 2 pine trees with bark boring insects, which was evident by the presence of dried resin outflows or small entry holes (~2mm in diameter) on the bark, divided by the total number of station vegetation plots (0.04 ha), for each site and year. Since vegetation surveys were conducted each year but beetles infect trees in late summer after nests fledge, I provide site-level densities of beetle-infected pine for each nest at two time periods: 1) when adult beetles and eggs were available to fledglings and adults in the late summer and winter following the nest (time t: adult beetle abundance), and 2) when developing larvae are beneath the bark, available to chickadees during the breeding season, but beetle eggs were laid in the year prior to the nest (time t-1: beetle larvae abundance). I predicted that adult beetle abundance later in the breeding season should be important to fecundity for fledgling survival, whereas beetle larvae abundance throughout the breeding season should improve nestling survival. Since I did
not measure the abundance of western spruce budworm directly at all sites and years, I used the per ha densities of host trees susceptible to budworm infestation for estimates of budworm availability: Douglas-fir and spruce trees that were decay classes 1 and 2 divided by the total number of 0.04 ha vegetation plots for each site and year. At three sites where station vegetation data were not collected, I used the total number of nest vegetation plots from nests of all cavity-nesting species to obtain mean per ha densities of beetle-infected pine, Douglas-fir and spruce trees.

Statistical analyses

I constructed five groups of mixed-effects models with the response variables expressed on a per nest level, including: Julian hatch day (calendar dates were converted to integers with 1 Jan as day one), number of chicks hatched, number of chicks fledged, rates of food delivery to nestlings (number of feeding trips per min), and the probability of nest survival (failed=0, fledged=1). The fixed-effects variables for possible inclusion in the models were: number of eggs laid (clutch size), Julian hatch day (excluded from models with Julian hatch day as the response variable), whether the nest was a first or second nesting attempt, cavity entrance size, cavity excavator type, nestling age (for feeding rate models only) and per ha densities of mountain chickadee, red-breasted nuthatch, red squirrel, Douglas-fir, spruce spp., and beetle-infected lodgepole pine. These variables showed significant effects on variation in hatch day, nest survival and nestling feeding rates; therefore I present the results of these three response variables, only.

Multiple nests in different trees occurred within sites; therefore, site was included as a random effect in all models. As some nest trees were used more than once across years, nest tree identity was included in all models as a random effect nested within sites to account for the
hierarchical error structure representing nest trees. To determine whether adult beetle or beetle larvae abundance was more important in influencing fecundity and nestling feeding rates, all fixed and random effects were held constant and fully-parameterized models with beetle abundance at time $t$ were compared to the counterpart models with beetle abundance at time $t-1$. All biologically relevant secondary interactions between predictor variables were examined.

I used linear and generalized linear mixed-effects models (Crawley 2007), and specified a normal distribution for the response variables hatch day and the number of nestling feeding trips, a Poisson distribution for number of chicks hatched and number of chicks fledged, and a binomial distribution for nest survival (nest fledged $\geq$ one young = 1, nest failed=0) models in the program R (version 2.12.1, R Development Core Team 2010). For models using the Poisson distribution the default log link was used, whereas the default logit link was used for models with the binomial distribution. Since nests found at different nesting stages can bias nest success estimates (Mayfield 1975), I applied a logistic-exposure adjustment to binomial distribution in nest survival models, which weights each observation based on the inverse of the number of days that the nest was observed, thus providing estimates for nest survival without assuming when nest loss occurs (Shaffer 2004). For nest survival models, I constructed two types of models comprised of either: 1) site characteristics and cavity entrance size, or 2) cavity formation type. Since more data were available for the former models, and the two types of models could not be compared without severely limiting the data set, I applied independent model selection techniques for each of the two models. Due to the hierarchical error structure of the observational data, penalized quasi-likelihood was used to calculate parameter estimates and standard errors for nest survival models (Bolker et al. 2009). For all models, the hierarchical errors were assumed to have normal distributions. For Poisson models, maximum likelihood estimates were obtained.
using Laplace approximation (Bolker et al. 2009). In overdispersed models (i.e., variance was not equal to the mean), penalized quasi-likelihood was used instead (Bolker et al. 2009).

Models for which maximum likelihood estimates are generated can be compared using an information theoretic approach using the Akaike’s Information Criterion (AIC) as the basis for model selection (Burnham and Anderson 2002). For each model, I calculated the AIC corrected for small sample sizes (AICc), the number of model parameters (K), and the total number of nests used (N) using the package MuMIn (Burnham and Anderson 2002, Bartoń 2011). I calculated the \( \Delta \text{AICc} \), which equals the AICc for the model of interest minus the smallest AICc for the set of models considered. The best model has a \( \Delta \text{AICc} \) of zero, but models with a \( \Delta \text{AICc} \) less than two suggest significant support from the data. I also calculated the Akaike weight of each model, and weights closest to 1 were the models with the most support from the data (Burnham and Anderson 2002). Thus, where the \( \Delta \text{AICc} \) value of the model with the next smallest \( \Delta \text{AICc} \) after the top model is greater than two, the top model can be used to make inferences of the fixed-effect variables on the response variables. I used Wald’s t- or Z-tests to determine whether each fixed-effect variable was significant given the other fixed-effect variables and the hierarchical error structure in the final models, and to progressively eliminate fixed-effect variables that did not significantly affect variation in nest survival, where likelihood ratio tests could not be used on quasi-likelihood estimates to select the best-fit model (Crawley 2007, Bolker et al. 2009).

In general linear mixed-effects models, the sign of coefficients indicate whether fixed-effect variables predict a positive or negative effect on response variables, given all other fixed-effect variables and error structure in the model (Crawley 2007). In logistic regression models, the coefficients are natural logs of the odds ratios (Kleinbaum et al. 1998, Crawley 2007). Thus, I used the parameter estimates of the final models to predict 1) whether fixed effects had a positive
or negative effect on hatch day and nestling feeding rates, and 2) how the odds of nest survival were predicted to change with levels in fixed effects given all other fixed-effect variables and hierarchical error structure in the model. Maximum likelihood and penalized quasi-likelihood estimates were obtained using the function lme in the package nlme, and the functions glmPQL in the library MASS, and logexp was used for quasipoisson and binomial models (Shaffer 2004, Bolker et al. 2009).

Results

In 15 years across 30 sites, I monitored 598 mountain chickadee nests, 117 of which I confirmed the nest to be a first or second attempt of the season. Second clutches (n=35) occurred in only four years, but 20 (57%) of those occurred in 2005, the peak of beetle larvae abundance, and 13 (37%) occurred in 2007. I confirmed clutch size in 189 nests, and determined nest fate for 300 nests, 225 (75%) of which fledged at least one nestling. Of the 75 failed nests, I found evidence for predation at 55 nests (nest was empty before 14 d post-hatch and the cavity was: usurped by a predator, torn open, or lacking nest material). The overall mean number of parental feeding trips to nests was 18 trips per hour, across 77 nests, at 19 sites, during 2004-2008.

Clutch size and nest phenology

Clutch size ranged between 4 and 10 eggs, with annual means ranging between 5.0 ± 1.4 eggs in 2004 and 7.3 ± 1.3 eggs in 2005, and an overall mean of 6.5 ± 1.4 eggs, per completed clutch (n=166, first clutches and unknown attempt number combined, but second nesting attempts excluded; Figure 4.1). Clutch size of second nests laid by pairs in the same breeding season ranged between 5 and 8 eggs, and the mean (6.1 eggs, n=23) did not differ from the overall mean.
clutch size (6.5 eggs; t=-1.27, p=0.21, df=187), but was about one egg smaller than known first clutches (7.1 eggs, n=42; t=-2.79, p=0.01, df=63).

Parameter estimates for the best-fit hatch day model predicted that clutch size declined with increasing latency in hatch day (Table 4.1). The incubation period ranged from 12-15 d in first (and unknown attempt number) clutches and 12-17d in second clutches, with an overall mean of 13 ± 1 d. The nestling period ranged from 16-21 d in first (and unknown attempt number) and 14-22d in second clutches, with an overall mean of 19 ± 1 d, indicating an overall mean nesting period of 30-34 days. Annual mean Julian hatch day ranged between 152 (1 Jun) ± 7.4 days in 2004 and 169 (18 Jun) ± 9.3 days in 2002, with an overall mean of 161 (10 Jun), but best-fit model parameter estimates predicted second clutches to hatch later than first clutches (Figure 4.1). Variables to best describe variation in hatch day were: clutch size, whether the nest was a first or second attempt, and site-level beetle larvae abundance and mountain chickadee densities. Best-fit model parameter estimates predicted hatch day to be later with increasing mountain chickadee densities but earlier with increasing clutch size and beetle-infected pines per ha. However, I found no significant fixed-effects variables in models describing variation in the number of chicks hatched or the number of chicks fledged.

**Nest survival**

The percent of nests to fledge at least one young ranged annually between 56% (of 27 nests) in 2002 and 88% (of 56 nests) in 2007 (Figure 4.1). The best-fit nest survival model predicted the odds of nest survival to decline by 93% (e^{-0.074}) with each unit increase in cavity entrance area, and by 18% (e^{1.69}) with each unit increase in red squirrel density, but to increase by 138% (e^{0.32}) with each unit increase in beetle larvae abundance (Table 4.2). The odds of a nest surviving was
2.4 ($e^{0.86}$) times higher in cavities excavated by downy woodpecker, and 2.0 ($e^{0.69}$) times higher in red-breasted nuthatch cavities, compared with those excavated by red-naped sapsucker (Figure 4.2).

**Nestling feeding rates**

The number of parental feeding trips to nests ranged between 4 and 52 trips per hour. Best-fit model parameter estimates examining variation in feeding trips showed a significant interaction between brood size and squirrel density: Feeding rates increased with an increasing number of nestlings, at sites and in years with lower than the mean density of squirrels (0.15 squirrels per ha; Figure 4.3a). However, at sites and in years with higher than mean squirrel densities, the number of feeding trips did not change with brood size. When chick age was removed from the model, I detected an interaction between beetle larvae abundance and brood size on feeding rates: feeding rates increased with brood size at sites and in years with low beetle larvae abundance, but increased only marginally with brood size at sites and in years with high beetle larvae abundance (Figure 4.3b).

**Discussion**

I found evidence to support the hypotheses that chickadee fecundity was influenced: 1) directly by food availability, 2) indirectly by nest sites and nest predation risk, and 3) by changes in nest predation risk resulting from the beetle outbreak. My main findings were that: 1) clutches were later in second nesting attempts and with increases in chickadee densities but earlier with increases in clutch size and beetle larvae abundance, 2) parents increased the rate of nest visits with increasing number of nestlings but only when squirrel densities were low, and 3) nest
survival declined with increases in squirrel densities, and cavity entrance size (in cavities excavated by larger-bodied excavators), but increased with increases in beetle larvae abundance.

**Food limitation and second clutches**

My findings that clutches were laid later at sites and in years with increases in chickadee densities but earlier-laid clutches were larger and that hatch day advanced with increases in densities of beetle-infected pine support the food limitation hypothesis. Earlier nests are often larger and have a higher probability of survival than later nests because insect emergence peaks early in the season, providing maximal food during the peak of nestling energy requirements for insectivores (Perrins 1965, Grant et al. 2005). But during high population densities, increases in territorial disputes over habitat patches with high food availability early in the breeding season can delay reproduction (Petit and Petit 1996). Since mountain pine beetle larvae and pupae were available from late summer after beetle eggs hatched until the following late summer when adult beetles emerged, food was available to residents throughout the year, including winter and early spring, and was earlier than other food such as Lepidoptera (including budworm; Reid 1962). Furthermore, the beetle outbreak was the largest on record for western Northern America, and the resulting superabundance of food may have alleviated competition for food (Martin and Norris 2007). This may have allowed chickadees access to increased food availability over winter for the upcoming breeding season, establish territories and initiate breeding earlier as a result of reduced territorial disputes, and feed larger broods earlier in the season. I suggest that nests were earlier when surrounded by high beetle larvae abundance because nestling food availability was higher, and adults were in better physiological condition earlier in the breeding season. Consequently, the greatest annual increase in mean clutch size occurred one year after the greatest increase in
adult beetle abundance (and therefore during the largest increase in larvae abundance), and the sharpest decline in clutch size followed the sharpest decline in beetle abundance (Figure 4.1). However, beetle abundance did not influence the relationship between chickadee density and hatch day, suggesting that the negative effects of density and the positive effects of food abundance operated independently on fecundity. Furthermore, a correlation between reproductive output and food abundance may not infer food limitation (Dhondt 2012). My result that reproductive output increased with beetle larvae abundance indicates that chickadee adjusted reproduction to food availability during the breeding season.

Second broods following successful first broods are rare in chickadees, and this is the first study, to my knowledge, to report mountain chickadee producing two successful nests within the same season in tree cavities (McCallum et al. 1999, Foote et al. 2010). In a nest-box study in California, second clutches of mountain chickadee ranged in size between 4 and 7 eggs, were ~ 2 eggs smaller than first clutches, and occurred in years with the largest clutches reported (Dahlsten and Copper 1979). Similarly, I found that 94% of second broods occurred in the years with the highest mean clutch sizes. However, I found slightly larger second broods (ranging between 5 and 8 eggs), and only a one-egg difference between first and second clutches. The result that 57% of second clutches occurred during the peak of beetle larvae abundance suggests that some double brooding may correlate with food supply, but that other factors, such as spring temperature may contribute to double brooding in other years (Dahlsten and Copper 1979). Second clutches may be initiated after either failed attempts or successful fledging of first broods (Lack 1954). The result that second clutches hatched significantly later than first clutches suggests that second broods were not re-nesting attempts, but initiated after first clutches fledged. However, incubation period was extended to 17 d in second broods (from an overall mean of 13 d
in first broods) and some parents were observed feeding fledglings of the first brood while attending the second nest (Norris unpublished data). For species in which multiple brooding is common, pairs that initiate earlier tend to have a second brood later in the season (Newton 1998), and food supplemented birds often show second brooding as a result of earlier nesting (Martin 1987, Arcese and Smith 1988, Nagy and Holmes 2005). I propose that earlier nests during year-round food pulses may lead to double brooding in mountain chickadee, but this may incur costs of delayed incubation periods.

**Nest site limitation and nest predation risk**

My finding that 73% of failed nests were due to predation supports the hypothesis that predation is the primary source of nest mortality, similar to other studies of mountain chickadee (Martin 1993, Dahlsten and Copper 1979). Even though red squirrel was the most abundant cavity-nesting mammal (Martin et al. 2004), I was unable to determine the predator species for most nests. Other rodents found in cavities in the area included: northern flying squirrel (*Glaucomys sabrinus*), bushy-tailed woodrat (*Neotoma cinerea*), short-tailed weasel (*Mustela erminea*), least chipmunk (*Tamias minimus*), and deer mouse (*Peromyscus maniculatus*; Martin et al. 2004). Cavities produced by small-bodied excavators could be easily accessed by the small-bodied predators such as chipmunks and mice, and tend to be in trees in greater states of decay, thus softer for larger-bodied predators to rip open to gain access (Martin et al. 2004). Yet larger cavities that are accessible without chewing or tearing required are often selected as nest sites for the larger-bodied, and most abundant predators, squirrels, woodrats, and weasels (Aitken et al. 2002, Martin et al. 2004). Since larger-bodied predators were more abundant than small-bodied predators, predator-prey encounter rates were likely higher in larger cavities (Martin et al. 2004).
To minimize nest predation risk, chickadee may avoid using larger cavities that are preferred by the most common predators and select small cavities, such as those produced by the small-bodied excavators, downy woodpecker and red-breasted nuthatch. The result that nest survival declined with increasing red squirrel densities and cavity entrance size indicates that squirrel presence was an accurate indicator of nest predation risk and that smaller cavities were safer from predation.

Reduced competition for safer nest sites can lead to improvements in fecundity for chickadees (Albano 1992). Mountain chickadee uses cavities most similar to red-breasted nuthatch, and both species occur at similar densities in British Columbia, suggesting that the two species compete for nest sites (Aitken et al. 2002, Norris and Martin 2010). However, nuthatch is a facultative excavator, and thus can avoid competition over old nests by excavating new cavities (Martin et al. 2004). In Chapter 2, I found that red-breasted nuthatch changed its excavating behaviour during the beetle outbreak, from using old cavities to excavating a greater proportion of its nests. As a result, competition for small cavities likely declined, allowing mountain chickadee to change its preference of cavities during the outbreak from using predominantly cavities excavated by red-naped sapsucker to using a greater proportion excavated by nuthatch and downy woodpecker (Norris et al. In Review). Since I found nest survival to be highest in the latter cavities, I suggest that reduced competition for safer cavities contributed to my observation of greater nest survival during the beetle outbreak.

**Interaction between food abundance and nest predation**

My result that the frequency of feeding trips increased with clutch size when squirrel densities were low, but did not increase when squirrel densities were high, suggests that the presence of squirrels limited nestling feeding rates. Adults must increase either the number of feeding trips or
prey load with increasing brood size in order to fledge more young per nest as shown in red-breasted nuthatch (Ghalambor and Martin 2000). I did not measure the quantity of food brought to nests and was thus unable to determine whether prey volume per trip increased with clutch size. However, the result that feeding trips did not increase with clutch size at sites and in years of high beetle larvae abundance, but fecundity increased nonetheless, suggests that parents exhibited plasticity in the ability to adjust prey volume per trip by bringing larger but less frequent loads when more food was available. Squirrel densities were correlated with declining nest survival and limited the frequency of feeding trips, suggesting that squirrel presence can reduce nest survival as a result of a reduction in nest visits, unless food supply is high.

Mountain chickadee parents can adjust the volume of food brought to nestlings, according to food availability surrounding nests, and when food availability is high, parents may spend less time foraging and more time defending nests from potential predators, leading to larger clutches and greater nest success (Grundel 1987, Zanette et al. 2003, Preston and Rottenberry 2006). In my study, squirrel densities and beetle larvae abundance were correlated at the site-level (Martin unpublished data); thus, my results that feeding trips did not increase with clutch size during high densities of squirrels and high beetle larvae abundance suggests that both food supply and predation risk may influence feeding rates similarly. When either squirrel densities or beetle larvae abundance were high, adults may have compensated for the reduced number of feeding visits by bringing larger prey loads. However, the model comprising squirrel densities best described variation in feeding rates when chick age was included in the model, suggesting that the model with squirrel densities was better supported by the data. In other studies, chickadee nest predation rates during high squirrel densities may be reduced if an alternate food source is available to squirrels (Mahon and Martin 2006). Thus, it is possible that squirrels switched from
foraging on bird nests to beetle larvae during the outbreak, and chickadees reduced the frequency of nest visits when squirrel densities (and beetle abundance) were high regardless of changes in predator foraging patterns. Also, habitat structure can influence nest survival (Fort and Otter 2004), and changes in habitat structure provided by the beetle outbreak may have led to some other indirectly positive effects on nest survival for chickadee. Nonetheless, chickadees responded to squirrel densities and beetle abundance by adjusting their feeding frequency, providing evidence of plasticity in parental effort in response to nest predation risk and food supply. This indicates that adults exhibited increased nest vigilance during the outbreak, which may have led to greater nest survival at sites and in years of high beetle larvae abundance.

Conclusion

In summary, the beetle outbreak led to increased fecundity and reduced nest predation, likely as a result of direct effects on food supply and nestling care and indirect effects of lower competition for safer cavities. My findings that food, nest predation risk, and nest sites influenced variation in fecundity of mountain chickadee support the hypothesis that all three factors interact to influence life history variation in birds (Martin 1995). This is the first study to examine how a secondary cavity nester responds to changes in these fundamental constraints, within the context of a community. These results highlight the importance of inter-specific relationships within communities and the direct and indirect effects of resource pulses, particularly for species dependent on others for reproduction, such as secondary cavity nesters. Further study of how the beetle outbreak influenced the relationship between nest site constraints and predation may reveal patterns in how resource pulses may influence the coexistence of competitors within disturbance-driven communities (Chase and Leibold 2003).
Table 4.1. Parameter estimates (Estimate), standard errors (SE) and degrees of freedom (DF) generated from the best-fit model describing variation in hatch day of 153 mountain chickadee nests, from 2000 to 2009, at 30 sites, in 106 nest trees, in interior British Columbia. Fixed effects were: no. eggs laid (clutch size), and whether the nest was a first or second clutch (second clutch), for each nest; and densities of beetle-infected pine (time $t-1$; Beetle larvae), Douglas-fir, spruce, mountain chickadee, and red squirrel, as detected on vegetation surveys and point counts at each site and year in which the nest was monitored. TreeID was nested within site as random effects in all models. Direction of parameter estimates indicates that hatch day became increasingly later (positive, +) or earlier (negative, -) with increases in the fixed effect, at the 0.1 level of significance shown in bold. See Appendix A for specific model selection results.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model Intercept</strong></td>
<td>180</td>
<td>4.8</td>
<td>76</td>
<td>37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Nest variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clutch size</td>
<td>-2.9</td>
<td>0.63</td>
<td>40</td>
<td>-4.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Second clutch</td>
<td>32</td>
<td>2.4</td>
<td>40</td>
<td>13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Site-level variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beetle larvae</td>
<td>-1.5</td>
<td>0.71</td>
<td>40</td>
<td>-2.1</td>
<td>0.044</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.045</td>
<td>0.15</td>
<td>40</td>
<td>0.29</td>
<td>0.77</td>
</tr>
<tr>
<td>Spruce</td>
<td>0.60</td>
<td>0.56</td>
<td>40</td>
<td>1.1</td>
<td>0.28</td>
</tr>
<tr>
<td>Mountain chickadee</td>
<td>9.8</td>
<td>5.4</td>
<td>40</td>
<td>1.8</td>
<td>0.079</td>
</tr>
<tr>
<td>Red squirrel</td>
<td>-3.9</td>
<td>5.7</td>
<td>40</td>
<td>-0.68</td>
<td>0.50</td>
</tr>
</tbody>
</table>
### Table 4.2. Results of best-fit logistic exposure models of the probability of nest survival (failed=0, fledged=1), as described by variation in a) site characteristics & cavity entrance size (181 nests), and b) cavity origin (153 nests), in central British Columbia. Parameter estimates, standard errors (Std. Error), and degrees of freedom (DF) produced from the models, using the logit link function, indicate the effects on nest survival, and the null hypothesis that the data do not support a relationship was tested using Wald Z test statistics (Z value), and associated p-values (Pr(>|z|)). Direction of parameter estimates indicates positive (+) or negative (-) effects on nest survival, with significant effects on nest survival at the 0.1 level of significance shown in bold. TreeID was nested within Site as a random effect in all models.

| Model type                                                      | Fixed effect     | Estimate | SE  | DF | Z value | Pr(>|z|) |
|----------------------------------------------------------------|------------------|----------|-----|-----|---------|---------|
| **a. Site characteristics & cavity entrance size**             |                  |          |     |     |         |         |
| Intercept                                                      |                  | 5.3      | 0.42| 177 | 13      | <0.001  |
| **Red squirrel**                                               |                  | -1.7     | 0.75| 177 | -2.3    | 0.024   |
| **Beetle larvae**                                              |                  | 0.32     | 0.18| 177 | 1.8     | 0.08    |
| **Cavity entrance area**                                       |                  | -0.074   | 0.027| 177 | -2.8    | **0.0059** |
| **b. Cavity formation**                                        |                  |          |     |     |         |         |
| Intercept                                                      |                  | 4.0      | 0.24| 149 | 17      | <0.001  |
| **Downy woodpecker**                                           |                  | 0.86     | 0.42| 149 | 2.0     | **0.041** |
| **Red-breasted nuthatch**                                      |                  | 0.69     | 0.41| 149 | 1.7     | **0.091** |
| **Natural decay**                                              |                  | 0.58     | 0.77| 149 | 0.75    | 0.45    |

*Nests in cavities of each form listed were contrasted with those excavated by red-naped sapsucker; positive parameter estimates indicate greater nest survival than nests in sapsucker cavities.

**Some nests were in cavities that were not excavated by birds, but instead were formed by natural decay processes (e.g., insect, fungal growth).
Figure 4.1 (next page). Annual variation in fecundity variables: a) mean number of eggs per nest in 166 mountain chickadee nests for which clutch size was confirmed; b) mean Julian Hatch Day (148 nests), and; c) percent of nests to fledge at least one fledgling (294 nests); and mean number of live lodgepole pine trees with sign of bark beetles per hectare surveyed at 30 forest sites in interior British Columbia. Known second clutches were excluded from fecundity variables. Error bars indicate standard errors of the means.
a) Clutch size

Mean no. eggs laid

Clutch size
Mountain pine beetle

Mean recent beetle-infected pine per ha

b) Hatch Day

Hatch Day

Mountain pine beetle

c) % Fledged

% nests to fledge ≥ 1 nestling

% Fledged
Mountain pine beetle

Mean recent beetle-infected pine per ha
Figure 4.2. Nest fate for 153 mountain chickadee nests in cavities of various origin from 1995-2009 in central British Columbia. Probability of survival in each cavity type differed significantly from nests excavated by red-naped sapsucker at the 0.1 level of significance (*), generated from the generalized linear logistic exposure model: \( P(\text{nest survived}) \sim \text{cavity origin} \) (see Table 4.2 for model results).
Figure 4.3 (next page). Food delivery rates by breeding pairs at 72 mountain chickadee nests across nests of varying clutch size (No. chicks in nest) at 17 sites with a) higher or lower than the mean densities of red squirrel (0.15 squirrels per ha; High squirrel, ●; Low squirrel, ○), and b) higher or lower than mean beetle larvae abundance (46 beetle-infected pine per ha; High beetle, ●; Low beetle, ○), as detected on point count surveys and vegetation plots, during 2004 to 2008. Lines are generated from the secondary interaction terms of a) clutch size and squirrel density ($\beta = -0.22 \pm 0.068$ SE, $p=0.0022$, df=53), in the best-fit general linear mixed model: No. trips ~ Squirrel density (RS) + Clutch size (CS) + Nestling age + CS*RS, and b) clutch size and beetle larvae abundance ($\beta = -0.16 \pm 0.075$ SE, $p = 0.042$, df = 68), in the simple linear model, No. trips ~ Beetle larvae abundance (B) + Clutch size (CS) + B*CS. See Appendix A for model selection results.
Figure 4.3a)

Figure 4.3b)
Appendix A

Table A.1. Model selection results for four models constructed to describe variation in hatch day of 153 mountain chickadee nests, from 2000 to 2009, in interior British Columbia. Variables included in models were: clutch size (CS), nesting attempt number (AN), and densities of mountain chickadee (M), red squirrel (RS), beetle-infected pine (B), live Douglas-fir (DF), and live spruce (Sx), and the hierarchical error structure Tree ID nested within Site. Aikaike’s information criterion, corrected for small samples (AICc) of the model that best described the variation in hatch day (had the lowest AICc score) was weighed against competing models, and explained significantly more variation where $\Delta$AIC < 3.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Fixed effects</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community + Habitat</td>
<td>CS + AN + M + RS + B + DF + Sx</td>
<td>1142</td>
<td>0</td>
<td>1</td>
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<tr>
<td>Community</td>
<td>M + RS</td>
<td>1264</td>
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<tr>
<td>Habitat</td>
<td>DF + B + Sx</td>
<td>1270</td>
<td>128</td>
<td>0</td>
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<tr>
<td>Null</td>
<td>Random effect only</td>
<td>1271</td>
<td>129</td>
<td>0</td>
</tr>
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Table A. 2. Model selection results (i), and parameter estimates of best-fit model (ii), for four models describing variation in food delivery rates by parents at 72 mountain chickadee nests across 17 sites in interior British Columbia, during 2004-2008. Fixed effects were: Number of nestlings (Clutch size; CS), nestling age (A) and site-level densities of red squirrel (RS), and beetle larvae (B). Tree ID was nested within Site for a hierarchical error structure in all models.

Aikake’s information criterion, corrected for small samples (AICc) of the model that best described the variation in feeding rates (had the lowest AICc score) was weighed against competing models, and explained significantly more variation where ΔAIC < 3. Direction of parameter estimates indicates positive (+) or negative (-) effects on feeding rates, and fixed effects are significant at the 0.1 level, in bold.

i) **Model-selection results for models describing variation in feeding rates**

<table>
<thead>
<tr>
<th>Model type</th>
<th>Fixed effects</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size + Age + Predation</td>
<td>CS + RS + A + CS*RS</td>
<td>-62</td>
<td>0</td>
<td>0.90</td>
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<tr>
<td>Null</td>
<td>Random effect only</td>
<td>-58</td>
<td>4.4</td>
<td>0.10</td>
</tr>
<tr>
<td>Food + Predation</td>
<td>B + RS + B*RS</td>
<td>-49</td>
<td>13</td>
<td>0</td>
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<tr>
<td>Food + Clutch size</td>
<td>B + CS + B*CS</td>
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<td>24</td>
<td>0</td>
</tr>
</tbody>
</table>

ii) **Parameter estimates of best-fit model describing variation in feeding rates**

<table>
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<tr>
<th>Fixed Effect</th>
<th>Estimate</th>
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<th>DF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model Intercept</td>
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<td>0.087</td>
<td>36</td>
<td>-0.92</td>
<td>0.36</td>
</tr>
<tr>
<td><strong>Red squirrel (S)</strong></td>
<td>1.1</td>
<td>0.38</td>
<td>13</td>
<td>2.8</td>
<td><strong>0.015</strong></td>
</tr>
<tr>
<td><strong>Number of nestlings (N)</strong></td>
<td>0.071</td>
<td>0.013</td>
<td>13</td>
<td>5.3</td>
<td><strong>&lt;0.001</strong></td>
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<tr>
<td>Nestling Age</td>
<td>0.0024</td>
<td>0.0033</td>
<td>13</td>
<td>0.73</td>
<td>0.48</td>
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<tr>
<td><strong>N x S interaction</strong></td>
<td>-0.23</td>
<td>0.067</td>
<td>13</td>
<td>-3.4</td>
<td><strong>0.0044</strong></td>
</tr>
</tbody>
</table>
Chapter 5. A double resource pulse of both food and nest cavities increases intra- and inter-specific competition in cavity-dependent insectivores in interior British Columbia, Canada

Resource pulses—brief, occasional, and intense events of high resource availability may permeate through multiple levels of terrestrial and aquatic food webs causing changes in population densities, inter-specific relationships, and/or individual behavioural patterns (Ostfeld and Keesing 2000, Yang et al. 2008). Most studies found that saturation of limited resources reduced competition among consumers (Yang et al. 2008). However, prior research examined species interactions at the trophic level only and few studies examined the mechanisms driving competition for multiple resources. Competition for resources within and between species may either increase or decrease, depending on how resource pulses influence the underlying behavioural mechanisms. For species limited by food and nest sites, direct competition for territories may increase if resource pulses improve foraging and nesting habitat, and increase the potential reproductive benefits to provide incentives for individuals to defend high quality nest sites (Territory Investment Hypothesis; TIH; Brown 1964, Fretwell and Lucas 1970). Increased intra-specific competition but decreased inter-specific competition may result from expanded niche breadths and reductions in inter-specific dominance of resource specialists over generalists (Ecological Niche Hypothesis; ENH; MacArthur 1958, Morse 1974, Chase and Leibold 2003). Finally, both intra- and inter-specific competition may decrease if individuals use the presence of conspecifics (Stamps 1988) or heterospecifics with the same habitat requirements (Mönkkönen et al. 1990) to assess territory quality in unpredictable environments (The Competitor Attraction Hypothesis; CAH). Inter-specific dominance hierarchies can even be reversed when dominants invade breeding territories of subordinates (Morse 1976), but the effects of spatial and temporal
variation in resource supply on the behavioral interactions underlying these reversals are rarely studied. Empirical studies of the effects of resource pulses on the nature and strength of inter-specific relationships may help to fill key gaps in community ecology (Agrawal et al. 2007).

Forest bird communities are often structured around complex inter-specific interactions of species that excavate tree cavities and other species that secondarily use those nest cavities (nest webs; Martin and Eadie 1999). Secondary cavity nesters are unable to excavate new nests and rely primarily on excavators, whereas facultative excavators can show plasticity in their excavation of new nests or reuse of existing cavities. As many excavators are also insectivores, large-scale insect outbreaks can lead to dual pulses in food and nest sites, influencing the competitive interactions among cavity-dependent insectivores. Recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) in western North America increased year-round food availability, and subsequently, population densities of many insectivorous birds, including many excavators (Otvos 1979, Westfall 2004, Martin et al. 2006).

Red-breasted nuthatch (*Sitta canadensis*) may either excavate or use an existing cavity for nesting, is primarily a bark forager, and populations increase in response to food pulses (Ghalambor and Martin 1999). Mountain chickadee (*Poecile gambeli*) is a secondary cavity nester that relies on other species and natural decay processes for nest cavities, and is primarily a foliage gleaner, but an opportunistic insectivore that can switch foraging substrate depending on forest insect abundance (McCallum et al. 1999). Both species have similar nesting requirements, using the smallest cavities in the nest web, and are the most abundant small-bodied cavity-nesting songbirds in interior British Columbia, Canada (Aitken et al. 2002, Martin and Norris 2007). The two species compete for cavities and have even reared young in the same nest cavity simultaneously (Robinson et al. 2005). Others have reported that nuthatches are consistently
dominant over chickadees (Wing 1946, Bock 1969, A. Grava pers. comm.). Both species exhibit aggressive behaviour towards conspecific and heterospecific individuals that threaten access to mates or food, which includes dominant individuals moving toward and supplanting their adversaries, and aggressive calls and displays that are unique to each species (Wing 1946, Minock 1972). Yet, chickadees use cavities excavated by nuthatches, and give alarm calls when predators are present, which nuthatches recognize and use to avoid predators (Aitken et al. 2002, Templeton and Greene 2007). Thus, under some circumstances, interactions between the two species may be mutualistic. As common residents in mixed coniferous-deciduous forests, both species forage in mixed species flocks in winter providing ample opportunity to either cooperate or compete for territories (Aitken et al. 2002, Mooney 2007).

Population densities of both species increased in response to the beetle outbreak (Norris and Martin 2010). Red-breasted nuthatch shifted nest site preference from areas of high nest site availability to those of high mountain pine beetle availability, where they excavated a greater proportion of nests (Norris and Martin 2008, Chapter 2). Mountain chickadee shifted cavity use from nesting primarily in cavities excavated by Red-naped sapsucker (Sphyrapicus nuchalis; a larger-bodied excavator) to those excavated by nuthatch and downy woodpecker during and after the beetle outbreak (Norris et al. In Review). In Chapters 3 and 4, I found that these shifts in habitat and cavity preferences led to increases in reproductive output for both species, and in Chapter 4 I hypothesized that increases in food availability could alleviate territorial disputes. However, the beetle outbreak also led to increased population densities of a common nest predator for nuthatches and chickadees, American red squirrel (Tamiasciurus hudsonicus; Martin and Norris 2007). Because increased predator presence can lead to reduced parental activity around the nest resulting in reduced fecundity (Fontaine and Martin 2006), high squirrel densities
may diminish territory quality and impede territory defense strategies. Thus, for both species, the beetle outbreak provided increases in reproductive benefits, the availability of smaller cavities, and densities of competitors and predators. Such changes in territory characteristics could lead to increases or decreases in agonistic behaviour within and between species.

I sought to determine how a dual pulse of food and nest sites resulting from an outbreak of mountain pine beetle influenced intra- and inter-specific interactions of two cavity-competitors that vary in their plasticity of bark beetle foraging strategies and excavation abilities, Red-breasted nuthatch, and Mountain chickadee. I used an experimental approach to infer the nature and strength of interactions within a population and among coexisting species (Martin et al. 1996, Martin and Martin 2001). I used territorial intrusion experiments of conspecifics and heterospecifics to determine how the beetle outbreak influenced the response of nuthatches and chickadees to territorial invaders. The Territory Investment Hypothesis predicts that high quality resources should be defended more aggressively; thus, both intra- and inter-specific aggression among nuthatches and chickadees should increase with beetle availability. However, the Ecological Niche Hypothesis predicts that intra-specific competition for access to mates should be higher when inter-specific competition for the resources that most limit both species is low (Chase and Leibold 2003). As a result, intra-specific aggression should increase with increasing beetle abundance, and inter-specific dominance of nuthatches over chickadees should be reduced, under the Ecological Niche Hypothesis. Finally, the Competitor Attraction Hypothesis predicts that mutualistic relationships should lead to declines in both intra- and inter-specific aggression with increasing beetle abundance (Figure 5.1).
Methods

Study area

I studied behaviour, fecundity, and habitat characteristics of cavity-nesting birds in 25 mixed coniferous-deciduous forest stands near William’s Lake, British Columbia, Canada (51°52’N, 122°21’W), from 2004-2008. The predominant deciduous species was trembling aspen (*Populus tremuloides*), and predominant coniferous species were Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*; hereafter, pine), and white and Engelmann hybrid spruce (*Picea glauca* x *engelmannii*; Meidinger and Pojar 1991). Study sites ranged from 15 to 32 ha (one 7-ha site) in size, and varied in composition from continuous forest to five sites that were comprised of a series of ‘forest groves’ (0.2 to 5 ha) within a grassland matrix. Additional study area and nest monitoring details are given in Martin and Eadie (1999) and Aitken et al. (2002).

Territorial intrusions

I used song playbacks with intruder simulations to investigate interference competition within and between species (Martin et al. 1996) during territory establishment and before eggs were laid until after chicks fledged, between 1 May and 30 June, during (2004-2005) and after (2006-2008) the beetle outbreak (i.e., five years of measurement). I simulated conspecific and heterospecific intrusions at nests that were active in the year of the presentation or inactive (nest sites active in previous years), and at random plots (on the territories ~50m from active or old nest; random-active, and random-inactive, respectively) to examine how territory characteristics (food and nest site availability, and population densities of community members) influenced territorial responses of nuthatches and chickadees. I compared responses measured at inactive nests to those at active
nests, belonging to both conspecifics and heterospecifics, to assess the level of territorial aggression. The two species exhibit unique behaviours with respect to aggressive calls and displays, but both species exhibit the same behaviour of moving towards and supplanting intruders (Wing 1946, Minock 1972). Therefore, I measured response to intruders by estimating the minimum distance (m) that a respondent approached each intruder during each simulated intrusion in order to examine a common behaviour and compare inter-specific responses. Each trial consisted of simulated intrusions of both species, presented in a random order. I used song recordings from the Peterson Field Guide audio compact disc (Cornell Lab of Ornithology 1992) in 2004, and during 2005-2008, I used recordings of songs of nuthatches and chickadees collected ~20 km outside the study area. Songs were digitally manipulated so that each song was 2 min in length, and projected at similar volumes, then transferred onto a portable media player and broadcast over speakers. A taxidermic model specimen (intruder) of the appropriate species was placed on a wire stand ~1m above the speakers, and presented with the appropriate song type for each trial, with a 5-min period of silence following each intruder species presented. For each respondent, I recorded the species, individual (if colour banded), sex, time of day, behaviour (attack, call, sing, swoop, etc.), and the closest distance (m) that they approached to the intruder. In cases where the respondent attacked the intruder, and aggression levels remained high, I waited ≥ 10 min to start the presentation of the next intruder species until the aggressive individual returned to displaying the behaviour observed before the intruder was presented. In 2004, Mountain chickadees showed significantly different mean distances approached to conspecifics compared to all other years ($F_{4,251}=5.17, p<0.01$), suggesting that the recordings of local chickadees elicited a different response from the Peterson’s recordings, so 2004 was excluded in analyses examining responses of Mountain chickadees. Nuthatch responses to
conspecifics in 2004 differed from those only in 2008 (F_{4,226}=5.34, p<0.01), therefore 2004 was included in all nuthatch analyses. Where intrusions were simulated at nest territories, I visually inspected the nest cavity using a pole-mounted video camera, and recorded fecundity characteristics (number of eggs or nestlings) and the stage of the nest (pre-nest, egg-laying, incubating, chick-rearing).

**Population densities**

In order to determine how population densities of conspecifics and heterospecifics (including predators) influenced the behavioural responses, I conducted point count surveys to estimate per ha population densities of mountain chickadee, red-breasted nuthatch, and red squirrel at 25 sites, during 2004-2008. In continuous forest sites, point count stations were spaced within a 100 m square grid ≥ 50 m from a grassland or wetland edge (one station ha^{-1}). Point count stations were placed at least 100 m apart in forest groves where trees were patchily distributed. From 0500-0930 hours, I recorded the species, and number of individual birds and squirrels detected within 50-m radius 6-min point counts at each station (7-32 stations site^{-1}). Each station across the 25 sites was surveyed three times (rounds) in each of the 5 years. Further details of population monitoring methods are provided in Martin and Eadie (1999). I divided the total number of individuals observed on all rounds by the total number of point counts to obtain estimates of mean individuals ha^{-1} for each site and year.

**Vegetation surveys**

To determine whether spatial and temporal variation in food and nest site availability influenced species interactions, I established 0.04-ha circular vegetation plots centered at point count station
every year during 2004-2008. For all trees ≥12.5 cm diameter at breast height (DBH; outside bark diameter measured at 1.3 m above ground) in each plot, I recorded tree species, DBH, general health (e.g., presence of boring insects on the bole), and decay class. Decay class 1 was a live, healthy tree, 2 a live tree with visible sign of bark boring insects or heart rot fungus, and 3-8 were standing dead trees in progressive states of decay (Thomas et al. 1979). Before and during the study period, an outbreak of mountain pine beetle occurred across all sites, with incidence of beetle attacks on pines increasing sharply after 2002, and by 2005 over 95% of the mature lodgepole pine trees (40% of the trees on the sites) were dead (Edworthy et al. 2011). However, the onset of the beetle outbreak showed temporal and spatial variation in the number of trees showing sign of beetle attack (Drever et al. 2009). Therefore, I examined the effects of beetle abundance at the site-year level. Beetle eggs are laid beneath the bark in late summer where they overwinter and beetle larvae complete development in the following summer before emerging as adults (Reid 1962). Thus, beetle larvae provided a rich food source throughout the winters and following breeding seasons for insectivores. I determined beetle-infected pine densities as the total number of decay class 2 pine trees with bark boring insects, which was evident by the presence of dried resin outflows, or small entry holes (~2mm in diameter) on the bark, expressed on a per ha basis divided by the total number of 0.04 ha vegetation plots, for each site and year. Since over 90% of nuthatch and chickadees nests were in aspen trees (Martin and Eadie 1999), I determined the densities of nest trees per ha from number of aspen trees divided by the total number of 0.04 ha plots, for each site and year.

**Statistical analyses**

I used the minimum distance (m) that a respondent approached each intruder during the territory
intrusion simulation as the metric of aggression. For both species, the data for minimum distance approached were heavily skewed toward zero and showed an uneven distribution in the number of response variables between 0-50 m. As a result of the truncated normal distribution and the high number of zero values, I applied a mixture of the binomial (for minimum distance = 0 or > 0) and left-truncated normal (for minimum distance > 0) distributions. I used linear mixed-effects models (Crawley 2007) to examine how variation in minimum distance approached was explained by the fixed-effects variables: intruder species (conspecific or heterospecific), territory type of the plot in which the experiment was conducted (active nuthatch nest plot, active chickadee nest, inactive nest, random-active nuthatch territory, random-active chickadee territory, or random-inactive), nest status of territory owners (if active nest plot), presentation sequence of intruders, and abundance of food (beetle-infected pine densities per ha for the corresponding site and year in which the intrusion experiment was conducted) and nest sites (nest-tree densities per ha), and densities per ha of red-breasted nuthatch, mountain chickadee, and red squirrel, and all biologically relevant secondary interaction terms. Because I conducted intrusion experiments at multiple locations (plots) within sites and at multiple sites within years, I included plot nested within site as random effects to account for the hierarchical error structure due to the repeated measures, in all models. Since the repeated measures were not evenly spaced within and between plots, I added a continuous autoregressive correlation within plots. These hierarchical errors were assumed to have normal distributions.

I used penalized quasi-likelihood (PQL) to generate parameter estimates (Bolker et al. 2009). I used Wald’s t-test to eliminate fixed-effects variables from fully parameterized models, and to determine whether fixed-effect variables had a significant effect on the response variables given the other fixed-effect variables and the hierarchical error structure in the best-fit (final)
model (Bolker et al. 2009). Positive signs of significant coefficients indicated that the minimum distance approached increased (the responding bird approached further distances) with increases in the fixed effect variables, and negative signs indicated that minimum distance decreased (i.e., the bird approached closer; Crawley 2007). Penalized quasi-likelihood estimates were obtained using the function glmmPQL in the library MASS, and all data analyses were conducted in the program R version 2.12.1 (Venables and Ripley 2002, R Development Core Team 2010).

**Results**

I conducted 974 territory intrusion experiments across 25 sites, during 2004-2009. I detected 397 responses (at least one adult detected <50 m from intruder) from the bark beetle generalist, Mountain chickadee (2004 excluded that involved an additional 39 responses), and 372 from Red-breasted nuthatch (bark beetle specialist). In some cases (Mountain chickadee, n=95; Red-breasted nuthatch, n=30) respondents struck the intruder, knocking it to the ground, and then repeatedly attacked the intruder until the observer removed it. Overall, both species showed similar responses to conspecific intruders (closest distance approached: Mountain chickadee, 9.1 m ± 0.77 SE; Nuthatch, 11 m ± 0.80 SE), but Mountain chickadees approached heterospecific intruders closer than did nuthatches (14 m ± 1.1 SE, and 21 ± 1.2 SE, respectively; Figure 5.2). During and immediately following the beetle outbreak (2004-2006), both species approached closer than the overall mean, and approached heterospecifics as close as the overall mean approach to conspecifics.
**Red-breasted nuthatch**

Consistent with the Ecological Niche Hypothesis, the final model describing variation in the minimum distance approached to intruders predicted that nuthatches approached conspecifics closer than chickadees ($\hat{\beta}_{NM} = -12 \pm 1.5$ SE; Table 5.1). As the densities of conspecifics increased, the minimum distance approached increased (individuals responded from greater distances). The relationship between response distance and beetle abundance depended upon whether the territory plot was active or inactive: Consistent with the Territory Investment Hypothesis, nuthatches approached intruders closer with increasing beetle abundance at active nuthatch territories (both at active nests and random plots ~50m from the nest; $\hat{\beta}_{Be\times NNP} = -37 \pm 21$ SE, $\hat{\beta}_{Be\times RNT} = -44 \pm 26$ SE, respectively), compared to territories that were unoccupied by both nuthatches and chickadees in the year of the experiment.

**Mountain chickadee**

In the final model describing chickadee responses to intruders, I found a significant interaction between beetle abundance and territory type (whether the experiment was conducted at an active or old nest, or a random plot within a chickadee territory; Table 5.2). On average, chickadees approached conspecific intruders closer than heterospecific intruders, ($\hat{\beta}_{NM} = 6.4 \pm 1.5$ SE), which supported the Ecological Niche Hypothesis. However, as beetle abundance increased, chickadees approached heterospecific intruders closer than conspecific intruders at active chickadee nest plots ($\hat{\beta}_{Be\times CNP} = -140 \pm 70$ SE; Figure 5.3), supporting the Territory Investment Hypothesis. Distance approached by chickadees decreased with increasing chickadee densities but increased with increasing nuthatch densities.
Discussion

I found support for both the Ecological Niche and Territory Investment Hypotheses at different spatial and temporal scales. Chickadees were more aggressive than nuthatches across all territories, sites, and years, consistent with the Ecological Niche Hypothesis. Niche breadth maintained inter-specific dominance hierarchies of resource specialists over generalists at broad spatial and temporal scales at the nesting guild level of resource specialization rather than the foraging guild. Both species were more aggressive to nuthatch intruders at active nest territories at sites and in years with increasing beetle abundance, suggesting that: 1) the more efficient beetle-foragers (nuthatches) may pose a greater threat to territory intrusion during beetle outbreaks, and 2) individuals increased their investment in territory defense with increases in food availability (Territory Investment Hypothesis).

Ecological niche hypothesis

My finding that responses to heterospecifics were stronger in chickadees than nuthatches (24% of responses by mountain chickadees led to an attack vs. 8% by nuthatches) contradicts previous observations that nuthatches are behaviourally dominant over chickadees (Wing 1946, Bock 1969, A. Grava pers. comm.). However these other studies were conducted at feeding stations, over winter, a time in which food is often severely limited for both species (Ghalambor and Martin 1999, McCallum et al. 1999). At the nesting guild, however, nest cavity resource specialists can behaviourally dominate generalists (Aitken and Martin 2008). For example, the secondary cavity nester, European starling (*Sturnus vulgaris*), can usurp cavities from excavating woodpeckers by initiating their nests before the woodpeckers do. Thus, Starlings are often
considered a behaviourally dominant species in the nest web (Ingold 1994, Aitken and Martin 2008). Similar patterns in dominance might be expected in Mountain chickadee, as populations increased in response to cavity supplementation suggesting that they were limited by cavity availability (Aitken and Martin 2012). In Chapters 3 and 4 I showed that Mountain chickadees initiate nests ~ 11d earlier than nuthatches, suggesting that earlier nesting facilitates indirect dominance of chickadees over nuthatches. Perhaps at the foraging guild, and in winter flocks, nuthatches dominate chickadees but during the breeding season when competition for cavities may be high, chickadees initiate nests earlier and exhibit higher levels of territoriality for nesting sites compared to nuthatch. Thus, my findings support the Ecological Niche Hypothesis.

An alternative explanation for my finding that chickadees dominated nuthatches is that the two species differed in their ability to recognize intruders as threats. Chickadees may have approached nuthatch intruders closer than nuthatches approached chickadee intruders because chickadees rely on nuthatches for providing nest cavities (Chapter 4) and must be able to respond to the presence of nuthatches for breeding. However, nuthatches rely on the mobbing calls of chickadees to indicate the presence of predators (Templeton and Greene 2007) and often approach chickadees closer than chickadees approach nuthatches at feeding stations and during winter (Wing 1946, Minock 1972), suggesting that nuthatches are adept at recognizing chickadees in other situations. Further work should examine the inter-specific interactions during winter to test the prediction that food constraints lead to nuthatches dominating chickadees in interior British Columbia.

**Competitor attraction hypothesis**

Since both species approached nuthatch intruders closest at active nest territories, and I began my
experiments before breeding was initiated, it is possible that both species used nuthatches as cues in territory establishment and the distance approached to nuthatch intruders represented territory prospecting rather than defense. However, I found that individuals that attacked the intruder, approached consistently closer than those that did not attack (In the simple linear model, Minimum distance ~ Attacker vs. non-attacker, for nuthatches, $\hat{\beta}_A = -16 \pm 3.3$ SE, $t = -4.7, p < 0.01$, and chickadees, $\hat{\beta}_A = -13 \pm 1.8$ SE, $t = -6.8, p < 0.01$) suggesting that the minimum distance approached indeed represented an aggressive response rather than a passive, exploratory response. Further, if individuals were using the presence of nuthatches to assess new territories, I would expect a closer approach to nuthatch intruders at all territories. Yet, both species approached similar distances to both nuthatch and chickadee intruders at heterospecific territories ($p>0.1$; Interaction effect of heterospecific nest plot and nuthatch intruder for both species), and the increased responses to nuthatch intruders were only observed at conspecific territories (Tables 5.1, 5.2), indicating territorial defense responses. Since distance approached was correlated with an aggressive response, and both species approached intruders closer with increasing beetle abundance, neither intra- nor inter-specific aggression was reduced with increases in food availability, as was predicted under the competitor attraction hypothesis. Thus, I was able to reject both the conspecific and heterospecific attraction hypotheses for both nuthatches and chickadees.

**Territory investment hypothesis**

Both species showed an increasingly aggressive response to all intruders at active territories, with increasing beetle abundance, suggesting that investment in territorial defense increased with the beetle outbreak (or more accurately, investment declined with reductions in beetle availability at
the temporal scale measured in this study). High levels of aggression and territorial defense often require elevated energy expenditures, but territories containing ample resources required for increased defense may also provide greater reproductive benefits as the energy spent on territorial defense is easily recouped (Martin 1987). In cavity-nesting Prothonotary Warblers (*Protonotaria citrea*), pairs occupying higher quality territories produced more fledglings and competitively excluded other pairs from territories (Petit and Petit 1996). Mountain pine beetles provide a year-round food source from after late summer when adult beetles lay eggs beneath the bark to the following summer when larval development is completed (Reid 1962). As both nuthatches and chickadees are winter residents, the beetle outbreak likely increased the energy reserves of individuals before the breeding season. During the beetle outbreak, nuthatches maintained a constant clutch size throughout the breeding season, and chickadees laid earlier and larger clutches, and had a higher probability of fledging nestlings (Chapters 3, 4). Thus, it is likely that territories with high beetle abundance provided more food resulting in higher fecundity, leading to an increase in territoriality before and during territory establishment in both species.

An alternative hypothesis to the Territory Investment Hypothesis is that conflicts escalated simply as a result of smaller territories and closer proximity to one another with high population densities and food availability, as was the case when food was supplemented to European nuthatches (*Sitta europaea*) in Sweden (Enoksson and Nilsson 1983). For chickadees, aggression may have been related to density-dependent effects, as individuals approached intruders closer at sites and in years with increasing chickadee densities. However, the declining responses of both nuthatches and chickadees with rising nuthatch densities, suggests that abundant nuthatches may even reduce territorial responses to intruders for both species. Nuthatch densities were among the highest in 2004 and 2007-2008, and lowest in 2005-2006 (Norris and
Martin 2010, Chapter 2), but both species showed the greatest responses to nuthatch intruders (closest distance approached) during years of lowest population densities (Figure 5.2). As nuthatch population densities increased with the beetle outbreak (Norris and Martin 2010), it was more likely that territories neighboured nuthatch pairs, and thus may have dampened the effect of intruders. The declining response of both species to rising nuthatch densities and the observation that annual variation in aggression to nuthatch intruders did not correspond with nuthatch densities suggests that even though population densities were higher and territories likely smaller during the beetle outbreak, high nuthatch densities did not directly elevate aggression levels.

Increased homogeneity in the distribution of resources generally results in increased inter-specific competition through dominance of resource specialists over generalists (MacArthur 1958). Previous experimental tests of the Ecological Niche and Territoriality Hypotheses revealed that indirect competition for food resources promoted ecological segregation and reduced direct territorial conflicts (Martin and Thibault 1996). At the foraging guild, the beetle outbreak increased the overall homogeneity in resources, but also increased the availability of nest sites, thus influencing species interactions at the nesting guild level, as well. In this scenario, the non-excavating and foraging generalist chickadee dominated nuthatches (the beetle specialist and excavator), suggesting that inter-specific dominance hierarchies observed at foraging guilds can be reversed when species differ in nest resource specialization. Increases in intra- and inter-specific competition with increases in beetle abundance suggests that behavioural mechanisms governing community structure may change dramatically during resource pulses that increase the disparity in territory quality. Close examination of behavioral interactions can allow detection of changes in the functioning of avian community dynamics as a result of resource pulses.
Table 5.1. Parameter estimates (Estimate), standard errors (SE), and degrees of freedom (DF) of the final mixture distribution (normal and binomial), linear mixed-effects model generated using penalized quasi-likelihood for minimum distance approached by Red-breasted nuthatches to simulated intruders of Red-breasted nuthatch (NM) and Mountain chickadee (CM), at various locations (plots) within territories of Red-breasted nuthatch and Mountain chickadee compared to random plots in inactive territories, with spatial and temporal variation in beetle abundance (beetle-infected pine densities; Be), and Nuthatch densities, across 114 plots at 25 sites in interior British Columbia, from 2004-2008. Estimates were generated from the final model, Minimum distance ~ Intruder + Beetle (Be) + Nuthatch density + Territory type (TT) + Be × TT; random effects = Site / Plot ID, with continuous autoregressive correlation within Plot ID. Fixed-effect variables had significant effects on distance approached to intruders where p<0.1, in bold. Although the responses in five classes of territory type were compared to those in random plots in inactive territories, only classes with significant effects are listed.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t-value</th>
<th>p-value</th>
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<tbody>
<tr>
<td>(Intercept)</td>
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<td>2.4</td>
<td>157</td>
<td>10</td>
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<tr>
<td>Nuthatch model (relative to CM)</td>
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<td>157</td>
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<tr>
<td>Beetle-infected pine density (Be)</td>
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<td>Nuthatch density</td>
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<td>TT: Random plot in nuthatch territory (RNT)</td>
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<td>3.1</td>
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<td>-1.5</td>
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<td>TT: Nuthatch nest plot (NNP)</td>
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<td>157</td>
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<td>Be x NNP interaction</td>
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<td>21</td>
<td>157</td>
<td>-1.8</td>
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Table 5.2. Parameter estimates (Estimate), standard errors (SE), and degrees of freedom (DF) of the final mixture distribution (normal and binomial), linear mixed-effects model, generated using penalized quasi-likelihood of minimum distance approached by Mountain chickadees to simulated intruders of Red-breasted nuthatch (NM) and Mountain chickadee (CM) at various locations (plots) within territories of Mountain chickadee and Red-breasted nuthatch compared to random plots in inactive territories, with spatial and temporal variation in beetle abundance (beetle-infected pine densities; Be), and nuthatch densities, across 112 plots at 25 sites in interior British Columbia, from 2005-2008. Estimates were generated from the final model, Minimum distance ~ Intruder + Beetle density (Be) + Chickadee density + Nuthatch density + Territory type (TT) + Be x TT; random effects = Site / Plot ID, with continuous autoregressive correlation within Plot ID. Fixed effect variables had significant effects on distance approached to intruders where p<0.1, in bold. Although the responses in five classes of territory type were compared to those in random plots in inactive territories, only classes with significant effects are listed.

<table>
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<th>Fixed Effect</th>
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<th>DF</th>
<th>t-value</th>
<th>p-value</th>
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</tbody>
</table>
Figure 5.1 (next page) a) Zero-net growth isoclines (solid lines) and directional changes in the population-level effects of intra- and inter-specific competition (dashed arrows) in species exhibiting population densities limited by cavity availability, Mountain chickadee (MOCH), and bark beetle availability, Red-breasted nuthatch (RBNU). MOCH competitively excludes RBNU at low levels of beetle and high levels of cavities and RBNU excludes MOCH at high levels of beetle and low levels of cavities. Intra- > Inter-specific competition during the dual resource pulse, promoting coexistence (adapted from Chase and Leibold 2003), and b) predicted changes in aggressive responses of each species to conspecific and heterospecific intruders with a dual pulse of mountain pine beetle abundance and nest sites. Aggressive responses are predicted to: i) increase with increasing beetle abundance as the energy and potential reproductive benefits for individuals to defend high quality sites increases (Territory Investment Hypothesis), ii) decrease towards heterospecifics but increase towards conspecifics, by expanding niche breadth, and reducing inter-specific dominance of resource specialists over generalists (Ecological Niche Hypothesis), or; iii) decrease towards both species as individuals use the presence of conspecifics or heterospecifics with similar habitat requirements to assess territory quality (The Competitor Attraction Hypothesis).
Figure 5.1a)

Figure 5.1b)

i. Territory Investment Hypothesis

ii. Ecological Niche Hypothesis

iii. Competitor Attraction Hypothesis
Figure 5.2. Annual variation in median closest distance approached by a) Red-breasted nuthatches, and b) Mountain chickadees to conspecific and heterospecific intruders, with overall means indicated by dashed lines, across 974 intrusion experiments conducted at 25 sites in interior British Columbia. Round brackets indicate the total number of responses elicited, and square brackets show the total number of intruder trials in each year (for both species), boxes show data within the 75th percentiles, whiskers show the maximum and minimum within the 90th percentiles, and circles show outliers.
Figure 5.3. Mean closest distance approached by respondent a) Red-breasted nuthatches and b) Mountain chickadees, to chickadee (CM) and nuthatch (NM) intruders across sites and years with increasing levels of beetle abundance, at active (solid lines) and inactive (dashed lines) territories occupied by conspecifics, in interior British Columbia, during 2004-2008 (2004 excluded in Figure 5.3b). Lines were generated from the linear models: Distance ~ Beetle (Be) + Territory type (TT) + Be × TT.
Chapter 6. General discussion and conclusions

Thesis Summary

Resource pulses are integral processes to the dynamics of many ecosystems, as species respond to direct effects of resource availability and to indirect changes in inter-specific interactions (Ostfeld and Keesing 2000, Yang et al. 2008). Globally, the greatest numbers of consumer responses to resource pulses are reported in temperate forests (Yang et al. 2010). Yet, little is known about the reproductive and behavioural mechanisms underlying the responses to the direct and indirect impacts within temperate forest communities (Yang et al. 2008, 2010). Ecosystem resiliency is suggested to be a major outcome of resource-consumer interactions that allows communities to sustain major perturbations.

Bark beetle outbreaks result in community-wide increases in food availability for many forest vertebrates and thus constitute major resource pulses affecting populations and communities in forest ecosystems (Ostfeld and Keesing 2000, Drever et al. 2008). In a community structured around the production of tree cavities for nesting, species that excavate their own cavities and forage on bark beetles can exploit novel habitats during bark beetle outbreaks (Chapter 2), to increase their fecundity despite increases in nest predator densities (Chapter 3). Secondary cavity nesters can also increase their fecundity in response to both the food pulse and the secondary pulse in cavities, through capitalizing on reductions in nest predation risk (Chapter 4). As a result of the high reproductive benefits offered by increased bark beetle availability, territories are defended more aggressively, resulting in increased intra- and inter-specific competition (Chapter 5). Overall, my thesis results suggest that plasticity in foraging and nesting niches allow cavity nesters to respond to pulses of bark beetles. The
increases in fecundity and territoriality suggest that species compensate both reproductively and behaviourally to capitalize on changes in resource supply and this results in altered community dynamics. Further research into the ecological determinants of plasticity in excavation, foraging, and territoriality behaviours may refine the predictions of species responses to resource pulses. Broadening the scope of these investigations to include resource pulses other than bark beetle outbreaks and temperate forests in different parts of the world will increase the robustness of these conclusions and lead to a better understanding of mechanisms underlying the observed responses. Below, I provide suggestions for future research to both refine the conclusions and broaden the scope of this research topic, nest web ecology and resource pulses, in general.

**Suggestions For Future Research**

**Refining conclusions of reproductive and behavioural plasticity in cavity-nesters**

Studies that examine how food limits breeding effort often report annual fluctuations in fecundity that corresponds with food supply (Boutin 1990, Dhondt 2012). In my study, fecundity increased at sites and in years with increasing beetle availability, but annual variation in reproductive output remained relatively stable for both species (Chapters 3, 4). Studies on European nuthatches (*Sitta europaea*) and tits (*Parus* spp.), species ecologically similar to North American nuthatches and chickadees, showed that improvements to territory quality may not lead to overall increases in fecundity (Enoksson and Nilsson 1983). Even though a greater number of territories were occupied during resource pulses, high gene flow among habitat types led to larger than expected clutches in poor quality habitat and smaller than expected in high quality habitat (Dhondt et al. 1990, 1992). Food-supplemented song sparrows (*Melospiza melodia*) in British Columbia showed an increase in multiple nesting attempts (Arcese and Smith 1988). I found a
greater number of second nesting attempts for both species, which has only been documented once before in nuthatches (Ghalambor and Martin 1999), and greater variation in fecundity variables for nuthatches, in the years of the beetle outbreak (Chapters 3, 4), suggesting higher variability in breeding strategies. I was unable to determine the effects of genetic variation, and breeding experience on fecundity. Finer scale demographic studies such as the effects of age and genetic plasticity might elucidate proximate mechanisms influencing annual variation in fecundity. Further examination of resource availability on these mechanisms may allow us to predict how resource pulses affect the variation in breeding strategies within populations.

Despite evidence indicating major disparities in fecundity between excavators and secondary cavity nesters, little is known about the selective pressures shaping the trait of facultative excavation (Martin 1993, Wiebe et al. 2007). As a result of the energy required early in the breeding season to produce new cavities, excavators often lay smaller clutches than secondary cavity nesters (Martin 1993, Mönkkönen and Martin, 2000, Wiebe et al. 2007). On the other hand, predators are less familiar with new cavities, thus these nests offer lower predation rates (Martin 1995). I found that nuthatches were able to exploit increases in beetle availability because they had the option of excavating cavities in novel habitats close to this food source, but overall, laid smaller clutches than secondary cavity-nesting chickdeees (Chapters 2, 3, 4). In addition, predation was the primary source of nesting mortality in both nuthatches and chickadees, suggesting that predation risk may influence nesting behaviour in both excavators and non-excavators more than was previously thought for cavity nesters (Chapters 3, 4). Thus, plasticity in excavation behaviour can allow rapid response to resource pulses shared with predators (Chapters 2, 3). Nuthatches exhibit other behaviours that are suggested to detract predators from nests, such as resin application to cavity entrances, but the effects of this anti-
predator behaviour on fecundity are unknown (Ghalambor and Martin 1999). Experiments to test how the presence of predators influences plasticity in excavation, and other predator avoidance strategies in facultative excavators may advance knowledge in the evolution of cavity excavation. Examining how resource supply influences the fecundity consequences of predator avoidance strategies may improve our understanding of top-down effects of resource pulses.

Generally, community-level predictions of resource pulses are often grounded in ecological niche theory, and thus competition for resources among consumers is predicted to decrease (Ostfeld and Keesing 2000, Yang 2004). However, studies that have contrasted niche hypotheses with hypotheses of territoriality (Martin and Thibault 1996) and competitor attraction (Mönkkönen et al. 1990, Forsman et al. 2009) show that behavioural mechanisms play a large role in territory establishment. Depending on these mechanisms, foraging niche overlap can result in either increased or decreased competition for pulsed resources. My study is the first to examine how these competing hypotheses can be used to explain the effects of resource pulses on inter-specific interactions at the levels of both nesting and foraging niches within a cavity-nesting community. Resource specialization at the nesting guild determined patterns in inter-specific dominance, which supported previous findings that cavity limitation leads to behavioural dominance (Aitken and Martin 2008), but also revealed reversals to patterns observed in nuthatches and chickadees at the foraging guild (Wing 1946, Bock 1969). My results that intra- and inter-specific competition increased with the beetle outbreak, and that inter-specific dominance hierarchies were reversed highlights the need for more experimental tests of the effects of resource availability and specialization on behavioural interactions within cavity-nesting communities. Supplementation of food and nest sites combined with behavioural
experiments may allow a more in-depth analysis of how resource specialization in both food and nest sites determine inter-specific dominance hierarchies within nest webs.

The effects of resource pulses in terrestrial ecosystems can persist for many years following the pulse, particularly at higher trophic levels (Yang et al. 2010). Reductions in food supply, but persistence of high quality cavities may allow continued alleviation of competition for cavities for generalist foragers, such as chickadees, to persist in the beetle-killed stands, but may not benefit the bark insectivorous nuthatches. Nuthatches exhibited stronger population declines following the beetle outbreak, compared to the generalist foragers, chickadees and squirrels (Norris and Martin 2010). Studies that have examined how cavity nesters recover following major disturbance events show that the structure and function of cavity-nesting communities may persist if cavity supply does not change (Drapeau et al. 2000, Drever et al. 2008). Yet, many cavity excavators are also bark insectivores, thus longer-term declines in cavity production may occur if population densities of excavators collapse and do not recover following the beetle outbreak (Edworthy et al. 2011). These long-term declines in cavity availability may not be observed for over a decade, as excavated cavities can persist for over 15 years (Cockle et al. 2011). Further work examining how long-term changes in cavity production and food supply following the beetle outbreak is needed to elucidate the feedback mechanisms and legacy effects of resource pulses.

**Broadening the scope of research on resource pulses in nest webs**

Resource pulses are driven by abiotic signals that trigger multiple ecological events (Ostfeld and Keesing 2000), thus the bark beetle outbreak was likely correlated with other changes in habitat conditions. One major contributing factor to mountain pine beetle (*Dendroctonus ponderosae*)
outbreaks was increasing temperatures in interior British Columbia (Aukema et al. 2008). These changes in climate are also predicted to increase drought stress and subsequently, mortality of trembling aspen (*Populus tremuloides*) trees in temperate forests of interior British Columbia (Hamann and Wang 2006), the primary nest tree species in nest webs in the region (Martin and Eadie 1999). As most woodpeckers prefer to excavate cavities in trees that are decaying, increased mortality of aspen may lead to short-term increases in nest-tree availability but longer-term declines as younger trees fail to develop into mature trees sufficiently quickly to replace fallen and unusable trees (Martin et al. 2004). In addition, rising temperatures can increase the susceptibility of forests to outbreaks of defoliators, such as lepidoptera spp. (Williams and Liebhold 1995), and seed masting events (McKone et al. 1998). At my study site, concurrent outbreaks of mountain pine beetle and western spruce budworm (*Choristoneura occidentalis*) led to positive synergistic effects on food availability in winter and summer, which correlated with a population-level boom and bust response by chickadees (Norris et al. In Review). The long-term consequences of temporal changes in the availability of nest trees and food as a result of climate change require further investigation.

Further examination of mechanisms regulating species coexistence within nest webs in other temperate forests will allow for broader implications of these findings. The majority of research on resource pulses is heavily biased towards the northern hemisphere, even though the same types of pulses have been reported in southern temperate forests (Yang et al. 2010). In Chile, climate-driven heavy rainfalls, seed masting events, and insect outbreaks can drive pulses in rodent populations and their avian predators (Feuntes and Campusano 1985, Lima et al. 2002). But, as in other studies of resource pulses, only the food web has been examined. Chilean temperate forests harbour guilds of cavity-nesting species that are ecologically very similar to
those examined in my thesis (Díaz et al. 2005, Altamirano et al. 2012). White-throated treerunners (*Pygarrhychas albogularis*) are bark insectivores that exhibit plasticity in excavation behaviour and Thorn-tailed rayaditos (*Aphrastura spinicauda*) are secondary cavity nesters that exhibit plasticity in foraging behaviour (Díaz et al. 2005, Altamirano et al. 2012). These two species compete for cavities with one another and with members of a very diverse, but poorly studied predator community, and thus their responses to resource pulses remain unknown. Given the apparent compositional and functional similarities of the British Columbian and Chilean nest webs, my findings may guide future research in southern temperate forests. Further examination of how resource specialization in both food and nest webs influences coexistence in Chilean species will provide general knowledge of community-level effects of resource pulses on wildlife species in temperate forests generally, information necessary for wildlife management of temperate forests in the Americas.

**Conclusion**

The response of cavity-nesting species to resource pulses may depend on their ability to exploit novel habitats, the degree of plasticity in foraging and nesting behaviours, and their interactions with competitors and predators. The mountain pine beetle outbreak increased fecundity of insectivores directly through increased food supply and indirectly through reducing the cost of excavation for facultative excavators and reducing nest predation risk in secondary cavity nesters. As a result of the increase in reproductive benefits, competition for territories increased and resource specialists (chickadees) dominated generalists (nuthatches) at the nesting guild. Even though cavity-nesting species showed plasticity in behavioural traits that allowed them to respond to rapidly fluctuating resources, the beetle outbreak lasted for only ~2-3 years. Long-term
changes in the availability of food and nests as a result of persistent, or multiple resource pulses may lead to negative impacts on communities. Examination of resource pulses at multiple levels of resource specialization and in other ecosystems can improve our understanding of how environmental variability affects wildlife communities.
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