

**TEMPORAL AND SPATIAL VARIATION IN HABITAT QUALITY:
BREEDING ECOLOGY OF THE CHESTNUT-BACKED CHICKADEE IN
UNCUT AND PARTIAL CUT FORESTS IN BRITISH COLUMBIA**

by

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ABSTRACT

I examined how partial cutting influenced the use and selection of habitat by chestnut-backed chickadees (*Poecile rufescens*). My objectives were: (1) to examine the variability of nest survival and identify the contributions of year, harvest treatment and habitat characteristics, and predator activity at 3 spatial scales, (2) to compare use and selection of nesting habitat in uncut, partial cut-mature, and partial cut-old sites at 3 spatial scales, and (3) to identify the influence of habitat structure or annual differences in food abundance and predation pressure on reproductive output.

I found that nest predation rates fluctuated between years: 56% in 2000, 64% in 2001, 10% in 2002, and 12% in 2003. Survival models revealed that only the covariate year reliably predicted nest survival time at the stand and nest patch scales, while year and nest height predicted survival time at the nest tree scale. I found no effect of harvest treatment in the stand, nest patch, and nest tree models. Squirrel population density, space use, and activity near nest areas did not differ between years. Indirect effects on nest survival may have occurred due to temporal changes in habitat quality for squirrels.

Chestnut-backed chickadees exhibited flexibility in resource selection when selecting nest sites. I found no correlation between the density of breeding chickadees and structural characteristics at the stand scale, but found selection of similar resources at the nest patch and nest tree scales. When selecting nest trees, chickadees in my system used a variety of tree species, conditions, sizes, nest site locations, and cavity types.

Reproductive output showed no consistent pattern across sites, and was highly variable among years. Chickadee foraging patterns differed between years suggesting annual changes in prey abundance and type, although reproductive output did not decrease with a decline in primary prey. Predators had the greatest impact on the daily

mortality rate of nesting chickadees. Indices of predator density did not differ among years; a functional response by predators due to changes in their food supply may have strongly influenced annual reproductive output of chickadees in this population.

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CHAPTER 1:

GENERAL INTRODUCTION

Habitat Use and Selection

Species may occupy different habitats as a result of population density, conspecifics and competitors, individual factors (dominance status, site fidelity, age), and changes in the availability of habitats and resources (Hildén 1965, Cody 1985, Newton 1998, Manly et al. 2002, Ahlering and Faaborg 2006). Correlations between habitat characteristics and bird abundance may not reflect habitat suitability because density can be a poor indicator of habitat quality (VanHorne 1983, Vickery et al. 1992).

Documenting habitat use in relation to availability to assess levels of selection (i.e., use that is disproportionate to availability) reveals only the amount of use or avoidance, not (1) why a particular resource or habitat is used, selected, or avoided, or (2) whether fitness measures (reproduction, survival) are affected (Manly et al. 2002).

Habitat selection is thought to occur at multiple scales in a hierarchical framework (Johnson 1980, Manly et al. 2002). This can be illustrated using forest songbirds as an example. During the breeding season, birds often select a breeding territory that includes suitable nesting and foraging habitat. Within the territory, birds may select a nest patch (area immediately around the nest) and foraging areas. Finally, birds select a nest tree, a specific location for their nest, within the nest patch (Figure 1.1). Investigating habitat selection at multiple scales is necessary because often we do not know which scale of selection influences the settlement patterns, space use, and fitness of birds. For example, many forest songbirds have low reproductive success due to high rates of nest predation by red squirrels (*Tamiasciurus hudsonicus*; Martin 1993, Sieving and Willson 1998, Tewksbury et al. 1998). Selection of suitable nesting habitat could occur at 1 or more

spatial scales; a nest site that is concealed or difficult to access, and/or a nest patch that is separated from high activity areas of squirrels.

Understanding habitat use and selection at multiple scales is also needed to make appropriate management decisions. Environmental variables (e.g., vegetation type) and the response of birds to these variables can be organized in a hierarchical structure (Orians and Wittenberger 1991, Esely and Bollinger 2001, Kristan 2006). Birds can respond to both fine-grained variables that exhibit change over a short distance such as within a bird's territory, and coarse-grained variables that exhibit change over longer distances, such as among territories or populations (Kotliar and Wiens 1990, Kristan 2006). Within forested habitats harvesting techniques can target individual trees (species, size, age, or decay class), groups of trees, or entire stands of trees. At the start of the breeding season birds may use the size, height, and crown size of individual trees to assess the amount of potential above-ground foliage density (and caterpillar density) within a potential territory (Marshall and Cooper 2004). Alternatively, birds may use the amount of continuous canopy observed when flying over a potential territory to assess quality. The former represents an assessment of fine-grained habitat features, while the latter represents an assessment of coarse-grained habitat features. Understanding the response of birds to both fine and coarse-scale habitat features may be needed to correctly interpret scale-dependent patterns in bird-habitat associations (Kristan 2006).

Researchers are often interested in understanding how patterns of habitat use and selection differ across a range of sites that differ in their suitability. This gradient of sites may be what most forest birds observe when selecting territories at a local or regional scale. Within forested landscapes, a variety of stand conditions may exist: uncut stands, low to medium intensity harvest stands (single tree or small group removal, variable

retention), and high intensity harvest stands (clearcut with retention). Recent evidence suggests that some cavity nesters can exhibit both flexibility in their use of resources (Walters et al. 2002, Hartwig et al. 2004) and resistance to habitat change (ability to overcome a change in habitat conditions) resulting from forest harvesting (Steventon et al. 1998, Leupin et al. 2004). How changes in forest structure influence the availability, use, and selection of habitat by forest birds can be examined by documenting patterns of selection in sites where the availability of resources (e.g., density of trees and snags, shrub cover) differs.

Temporal Variation in Habitat Conditions

Habitat suitability for forest birds can also differ between years due to short-term changes in resource availability. Many terrestrial ecosystems are characterized by pulsed resources, the temporary availability of high levels of resources that become depleted with time (Ostfeld and Keesing 2000). Pulses of seeds can be elicited by regional or global climatic fluctuations including El Nino southern-oscillation (ENSO) events which can cause increased rainfall or solar radiation (Ostfeld and Keesing 2000). ENSO events have also been linked to higher arthropod biomass in deciduous forests in New Hampshire (Sillet et al. 2000, Holmes and Sherry 2001). The presence of pulsed resources can influence habitat conditions directly by increasing a critical or limiting resource (e.g., increase in food availability), or indirectly by altering community structure and function (e.g., changes in predator-prey relationships, numerical and functional responses of prey and predator).

Pulsed resources resulting from insect outbreaks can increase food availability for insectivorous forest birds. Outbreaks of defoliating caterpillars (Lepidoptera) can elicit both numerical (Holmes et al. 1986, Holmes and Sherry 2001, Jones et al. 2003) and

functional responses (Connor et al. 1999, Tremblay et al. 2003) in forest birds. Pulses of defoliating caterpillars can also increase the reproductive output (number of young fledged) of insectivorous bird species (Sillet et al. 2000, Tremblay 2003). Pulsed resources can also set off a complex chain of reactions that can have a significant impact on food webs in forest ecosystems (Ostfeld et al. 1996). Long term studies in oak forests in the eastern United States have found that seed produced by oaks has cascading effects on communities including the mice and deer that feed directly on the seeds, the ticks that live on the mice and deer, and the viruses spread by the ticks (Ostfeld et al. 1996). In years of high acorn production, rates of nest predation on artificial nests (McShea 2000), small mammal populations, and nest predation rates on forest songbirds all increased (Schmidt et al. 2001, Schmidt 2003). Complex species interactions triggered by acorn mast events resulted in 2 negative effects on forest songbirds: nest predation by rodents, and predation on fledglings, juveniles, and adults by hawks (Schmidt and Ostfeld 2003). In New Zealand, stoats (*Mustela erminea*) preyed on nestlings of endemic birds after a decrease in the availability of mice and rats (King 1983). Following years of masting beech crops, rodent and stoat densities responded numerically until rodent numbers crashed and stoats switched from mice and rats to birds.

Red squirrels are generalist consumers and can forage on a wide variety of food items including seeds, buds, fruits, fungi, insects, birds, and small mammals (Banfield 1974, Callahan 1993, O'Donoghue 1991). These items differ in their resource quality and availability, including seeds from conifer cones (high resource quality, unstable availability), and fungi, fruit, and buds (low resource quality, stable availability). Temporal variation in red squirrel habitat quality resulting from fluctuating levels of resources may play an important role in annual rates of nest predation for many forest

songbirds. Within forest habitats, the composition and abundance of mast-ing conifer species results in differences in seed availability over time and space (Koenig and Knops 2000). In addition, regional scale climatic fluctuations could influence the production of conifer seeds. The annual abundance of cone crops is related to squirrel population density (Smith 1968, Kemp and Keith 1970) and reproductive success (Rusch and Reeder 1978, Wheatley et al. 2002). Although red squirrels primarily consume and cache seeds from conifer cones, they are also important predators of forest songbirds (Martin 1993, Sieving and Willson 1998, Tewksbury et al. 1998). Squirrels may exhibit numerical (Martin and Joron 2003) or possibly functional responses to changes in seed production, resulting in high annual variation in nest predation rates for many forest songbirds.

Ecology of the Chestnut-backed Chickadee

The chestnut-backed chickadee (*Poecile rufescens*) is a small, cavity nesting resident bird of western North America. There are currently 3 recognized subspecies, the ancestral form (*P. r. rufescens*) and 2 subspecies that occur only in California (*P. r. neglectus* and *P. r. barlowi*; Dahlsten et al. 2002). Chickadees are members of the family Paridae, a diverse group of species exhibiting considerable ecological isolation when compared to the sympatric species of the genus *Parus* in Europe (Smith 1967). Exceptions in North America include the overlap of the black-capped chickadee (*P. atricapillus*) with the Carolina chickadee (*P. carolinensis*) in the southeast, the mountain chickadee (*P. gambeli*) in the west, and the chestnut-backed chickadee in the Pacific northwest (Brennan and Morrison 1991, Smith 1991). Mountain and chestnut-backed chickadees are sympatric in areas of British Columbia, Washington, Oregon, California, Idaho, and Montana (Brennan and Morrison 1991). Chestnut-backed chickadees share morphological, behavioural, and ecological traits with other “brown-capped chickadees”

such as the boreal chickadee (*P. hudsonicus*) and possibly the gray-headed chickadee (*P. cinctus*), as opposed to “black-capped chickadees” which include the Mexican (*P. sclateri*), Carolina, mountain, and black-capped chickadees (Smith 1991, Dahlsten et al. 2002). Recent genetic evidence has shown *P. rufescens* and *P. hudsonicus* to cluster with *P. sclateri* (Gill et al. 1993). Similarities among these 3 species include use of peripheral forest habitats (forest habitats at the outer edge e.g., coastal, northern boreal) and similar vocal characteristics (calls have nasal quality, no whistled song; Dahlsten et al. 2002).

Chestnut-backed chickadees are found in humid coastal and interior forests from south-central and southeastern Alaska to central California, a long, narrow distribution of approximately 3200 km. In the continental interior, this species occurs from southern British Columbia and western Alberta through mountainous areas in northern Idaho, northwest Montana, eastern Washington, and northeastern Oregon (Dahlsten et al. 2002). Chestnut-backed chickadees also occur sporadically in the central interior of British Columbia, along the western slopes of the Coast Ranges and along major river valleys such as the Skeena and Kispiox (Campbell et al. 1997). The geographic range of this species has expanded during the past 5 decades into the central Sierra Nevada and suburban areas in eastern San Francisco Bay (Dahlsten et al. 2002).

During the non-breeding season, chestnut-backed chickadees appear to form winter flocks and establish group territories in a manner similar to other species within this genus (C. L. Mahon, personal observation). Black-capped chickadees form stable flocks during the winter (Smith 1984, 1991), possibly to defend winter food supplies, or to control access to mates or nest sites (Smith and Buskirk 1988). Flock size can vary, but often consists of 4-5 mated pairs and unmated adults and juveniles (Smith 1991). Chestnut-backed chickadees can also form mixed-species feeding flocks with red-

breasted nuthatches (*Sitta canadensis*) and brown creepers (*Certhia americana*) during winter, early spring, and late summer and with golden-crowned kinglets (*Regulus satrapa*) in late summer (C. L. Mahon, unpublished data).

During the breeding season in British Columbia, this species is found at elevations from near sea level to 1350 m on the coast and from 500 m to 1450 m in the interior. Along the coast, it is the characteristic breeding chickadee of mature coniferous forests containing western hemlock (*Tsuga heterophylla*), mountain hemlock (*T. mertensiana*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), coastal Douglas-fir (*Pseudotsuga menziesii* ssp. *menziesii*), and grand fir (*Abies grandis*). On Vancouver Island, the Gulf Islands, and the Queen Charlotte Islands, chestnut-backed chickadees nest in riparian and deciduous forests, as well as drier, open habitats that contain Douglas-fir, Garry oak (*Quercus garryana*), and arbutus (*Arbutus menziesii*). In the interior, the chestnut-backed chickadee breeds mainly in the wet valleys of the Interior Cedar-Hemlock (ICH) biogeoclimatic ecological zone in northwest and southeast British Columbia (Campbell et al. 1997). Pairs settle out of winter flocks and establish breeding territories which can range in size from 1.3 to 14.6 ha (average = 4.5 ha, $n = 87$) in conifer-dominated mature forests (C. L. Mahon, unpublished data). Pairs aggressively defend breeding territories from other pairs and defend nest areas from competitors like red-breasted nuthatches (C. L. Mahon, unpublished data). During pre-incubation and incubation, chestnut-backed chickadee pairs display pair-bonding behaviour typical of other species in this genus such as exploring cavities in trees, excavating a nest cavity, and mate-feeding (Smith 1993, Hailman and Haftorn 1995, Ficken et al. 1996, McCallum et al. 1999).

The chestnut-backed chickadee is a facultative weak cavity excavator that uses diseased, dead, or dying trees with decaying wood for nesting (Zarnowitz and Manuwal 1985, Dahlsten et al. 2002). Multiple nest cavities can be partially excavated before 1 nest site is selected and excavation is completed (C. L. Mahon, unpublished data). Once a nest site is selected, both members of the pair excavate the nest cavity. Little information exists on specific requirements at the nest patch and nest tree scales because all prior breeding ecology studies used nest boxes (Grundel and Dahlsten 1991, Kleintjes and Dahlsten 1994, 1995). Chestnut-backed chickadees breeding in northwest British Columbia use a wide variety of tree conditions and sizes, nest site locations, and cavity types (Chapter 3). Average clutch size is 6-7 eggs (Dahlsten et al. 2002) with pairs attempting to renest after early season failure and raise second broods after a successful first nest (C. L. Mahon, unpublished data).

Chestnut-backed chickadees forage predominantly on foliage high in the canopy of live conifer and deciduous tree species (Airola and Barrett 1985, Weikel and Hayes 1999), although they can also forage on shrubs in the subcanopy (Weikel and Hayes 1999, Dahlsten et al. 2002). Chickadees are flexible in their use of substrates, responding rapidly to short-term changes in the spatial distribution of their prey (Robinson and Holmes 1982). Chestnut-backed chickadees use arthropods (65% of total year-round diet), seeds, and plant material (35% of total diet) to meet dietary requirements (Dahlsten et al. 2002). During the breeding season, nestlings are fed the larvae of needle-foraging insects and larvae from the order Orthoptera and Hymenoptera (Kleintjes and Dahlsten 1992, 1994).

Thesis Objectives

Chestnut-backed chickadees are suited to examine how small-scale changes in forest structure may influence habitat use patterns because they occupy moist forest types that are dominated by frequent, small-scale disturbances like wind, insects, and disease as opposed to large-scale fires (Heijl et al. 2002). In forests containing many disturbance agents, large areas of the stand may be affected due to high frequencies of both small (single or group tree mortality) and large (windthrow areas > 0.5 ha) disturbance events. Birds inhabiting these forest types may show resistance to openings in the canopy created by harvesting because these simulate natural disturbance events operating within stands (Steventon et al. 1998, Chambers et al. 1999, Robinson and Robinson 1999, Leupin et al. 2004).

I conducted a 4 year study using a multiscale approach that included a range of spatial scales (breeding territory, nest patch, nest tree) over which chickadees were likely to respond to changes in habitat heterogeneity and resource availability. To examine nest predation as an interaction between prey, predators, and the environment, I first examined how nesting habitat, predator activity, and year effects influenced chestnut-backed chickadee nest survival. I then examined how the availability of critical attributes influenced the selection of nest patch and nest tree habitat and the density of breeding pairs across sites. The availability of critical attributes like unhealthy trees may limit populations of cavity nesting birds. If a threshold level of critical attributes is maintained across sites, then density (pairs/ha) may be similar across sites as represented by the straight line in Figure 1.2. If critical attributes decrease across sites and become limiting, density may decrease (curved line in Figure 1.2). Finally, I attempted to assess fitness consequences of habitat selection patterns by determining whether 1) nesting habitat

selected at the nest patch and nest tree scales, or 2) suitable foraging areas and predation pressure within breeding territories had the largest influence on reproductive output of chickadees. Foraging areas and their associated food supply, and predator abundance can vary temporally resulting in direct (e.g., increase in food availability) and indirect (e.g., change in predator-prey relationship) influences on habitat conditions.

My objectives were:

- 1) To examine the variability of chestnut-backed chickadee nest survival and identify the contributions of year, harvest treatment and habitat characteristics, and predator activity at 3 spatial scales (stand, nest patch, nest tree; Chapter 2);
- 2) To describe and compare the characteristics of uncut sites to structurally modified partial cut sites (Chapter 3);
- 3) To compare use (stand scale) and selection (nest patch, nest tree scales) of chestnut-backed chickadee nesting habitat in uncut, partial cut-mature, and partial cut-old sites (Chapter 3); and
- 4) To determine whether habitat structure or annual differences in food abundance and predation pressure had the largest influence on the annual reproductive output of chestnut-backed chickadees (Chapter 4).

Study Area and Study Sites

The McCully Creek watershed is located in northwest British Columbia, Canada ($55^{\circ}22' \text{ N}$, $127^{\circ}50' \text{ W}$), approximately 35 km north of the town of Hazelton in the Interior Cedar-Hemlock moist cold (ICHmc) biogeoclimatic ecological subzone (150 to 1000 m elevation) within the coast-interior transition area in northwest British Columbia (Banner et al. 1993; Figure 1.3). Mature forest stands within this temperate, humid environment were dominated by western hemlock but also included western redcedar,

subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), hybrid spruce-the complex of Sitka spruce, white spruce (*Picea glauca*), and Engelmann spruce (*P. engelmannii*)-, paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and black cottonwood (*P. balsamifera*). Amabilis fir (*Abies amabilis*) also occurred at higher elevations. Old-growth forests were dominated by western hemlock with major components of sub-alpine and amabilis fir, and western redcedar. Zonal ecosystems consisted of a thick moss layer dominated by feather mosses and a poorly developed herb and shrub layer (Coates et al. 1997). Natural disturbance patterns in the ICH are characterized by frequent small-scale, gap forming disturbances operating at the individual tree scale (Coates and Burton 1997). Treefall gaps of various sizes are created by natural tree mortality, wind, fungi, and insect attack (Banner et al. 1993). Important diseases include heart rots like red ring rot (*Phellinus pini*), red belt fungus (*Fomitopsis pinicola*), and Indian paint fungus (*Echinodontium tinctorium*), and root rots like Tomentosus root rot (*Inonotus tomentosus*) and Schweinitzii butt rot (*Phaeolus schweinitzii*), while insects include mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*D. rufipennis*), western balsam bark beetle (*Dryocoetes confusus*), western hemlock looper (*Lambdina fiscellaria lugubrosa*), green-striped hemlock looper (*Melanolophia imitata*) and two-year-cycle budworm (*Choristoneura biennis*).

I monitored 3 uncut sites and 5 partial cut sites (19-24 ha) ranging from low intensity (30% of the stand volume removed as single trees and small patch cuts), to high intensity harvest (60% of the stand volume with 30% in openings of 0.1 ha to 0.5 ha and 30% as single trees between openings; Coates et al. 1997) within the McCully Creek watershed (Figure 1.3). Study sites represented a gradient of stand conditions containing small and large treefall gaps surrounded by a matrix of uncut or thinned forest (single tree

removal). Uncut sites contained a few small natural gaps, while partial cut-mature sites contained small gaps (e.g., 30% volume removal) or small to large harvested gaps (40% and 60% removal) surrounded by thinned forest. Partial cut-old sites contained both natural and harvested gaps within a thinned forest matrix, with gap sizes ranging from small to large depending on harvest intensity and natural disturbances found within sites. In partial cut sites, trees were removed across all species and diameter classes. Sites were within mature (145 years) and old-growth (353-373 years) forest stands at elevations ranging from 455-665 m, with time since harvest for partial cut sites ranging from 3 to 8 years.

Overview of Thesis

In chapter 1, I introduced the challenges associated with conducting studies of habitat use and selection for forest birds. I presented examples of how temporal variation in habitat conditions can result in direct and indirect effects on songbird populations. I described the ecology of the chestnut-backed chickadee and what is known about its breeding ecology in British Columbia. This background information described why chestnut-backed chickadees were suited to examine responses (i.e., habitat use, behaviour, reproduction) to small-scale changes in habitat structure.

In chapter 2, I examined the variability of chestnut-backed chickadee nest survival and identified the contributions of year, harvest treatment and habitat characteristics, and predator activity at 3 spatial scales (stand, nest patch, nest tree). I presented data on nest survival time, causes of nest failure, habitat characteristics, and predator activity (density and space use). I used an information-theoretic approach to develop sets of candidate models at each scale and determined support for my hypotheses that nest survival time of chickadees differed between years, and as a result of harvest treatment, habitat

characteristics, and predator activity. I then explored the possible role of pulsed resources in exerting strong influences on predator-prey communities.

In chapter 3, I described and compared habitat attributes of uncut sites to structurally modified partial cut sites. I then examined the use (stand scale) and selection (nest patch, nest tree scales) of nesting habitat for chestnut-backed chickadees in uncut, partial cut-mature, and partial cut-old sites. I assessed habitat use at the stand scale by examining correlations between stand characteristics and breeding density. I examined selection at the nest patch and nest tree scales by comparing used resources to available resources within chickadee territories. I then discussed whether flexibility in use of resources and resistance to habitat change were traits associated with species inhabiting forest types characterized by small-scale disturbances.

In chapter 4, I determined whether habitat structure or annual differences in food abundance and predation pressure had the largest influence on the annual reproductive output of chestnut-backed chickadees. At each site, I summarized data on foraging patterns to determine if changes in prey abundance altered habitat use patterns and behaviour, and used an index of squirrel activity as a measure of predation pressure. I determined differences between successful and depredated nests using habitat structure variables. I then discussed how temporal changes in the availability of resources can alter the condition or quality of habitat for birds and their predators.

In chapter 5, I summarized my results and discussed the influence of temporal variation on community interactions and the importance of understanding habitat use and selection at multiple scales. I also examined why chestnut-backed chickadees exhibited resistance to habitat change created by partial cutting.

Chapters 2, 3, and 4 are written as stand alone papers.

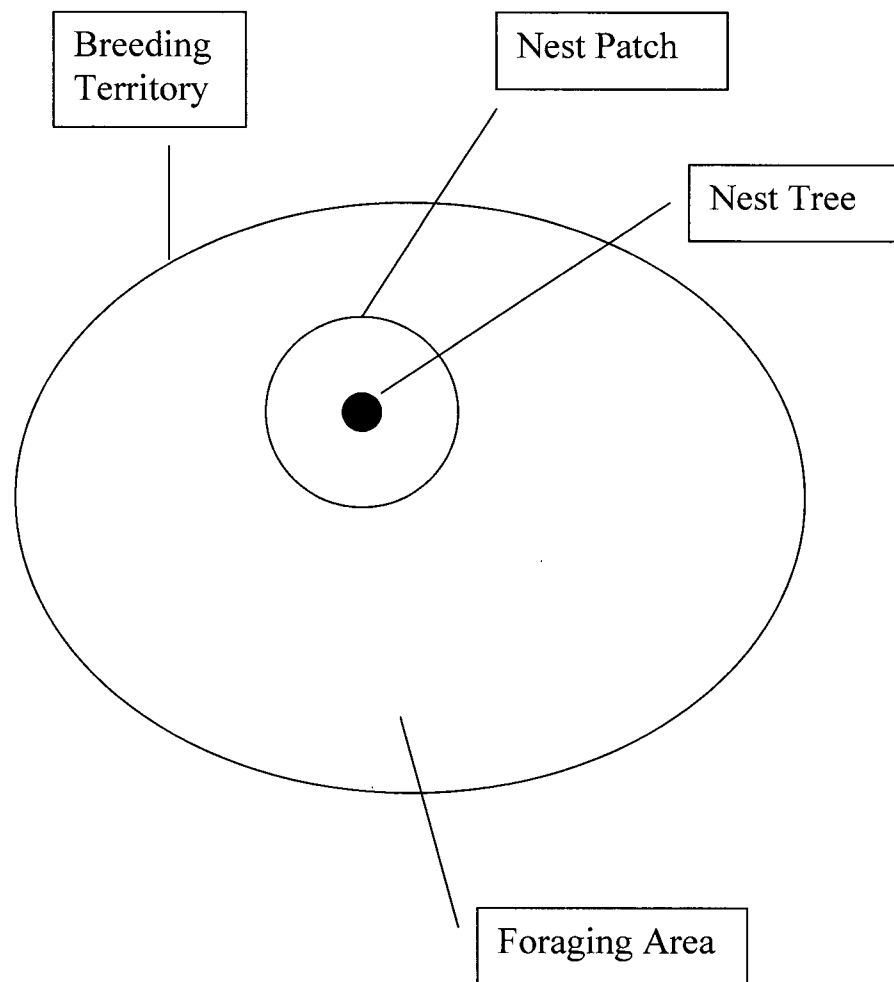


Figure 1.1. Hierarchical framework of habitat selection for forest birds.

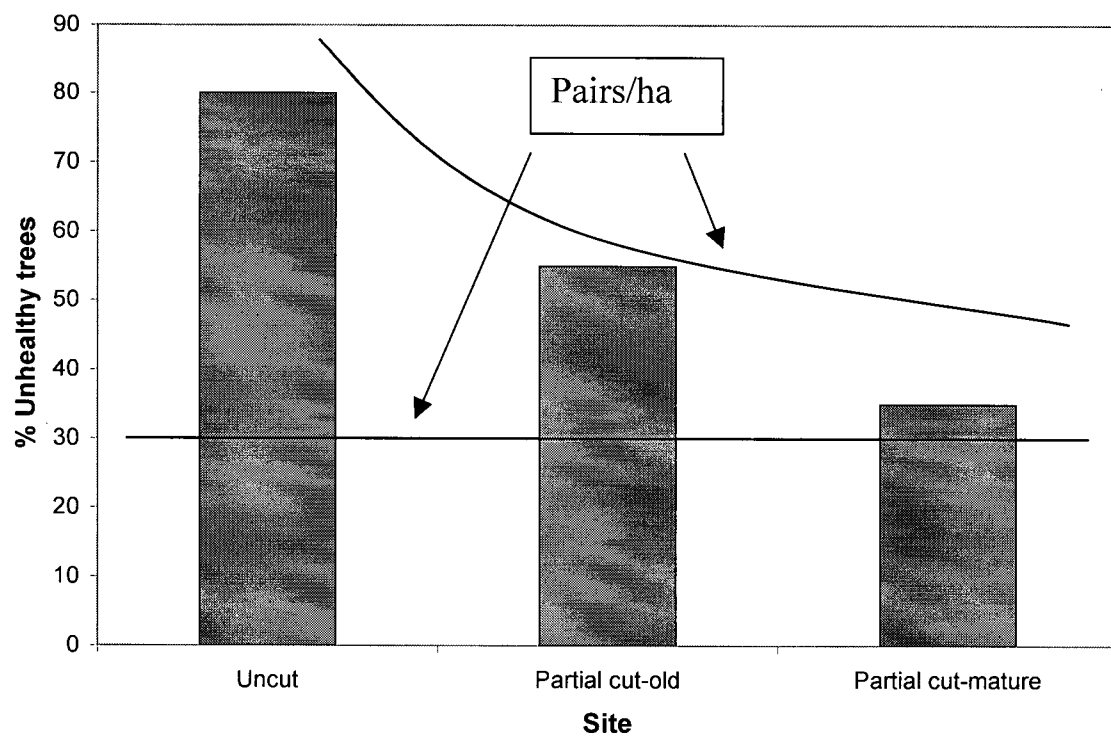


Figure 1.2. Predicted responses by chestnut-backed chickadees to changes in the availability of critical resources (unhealthy trees).

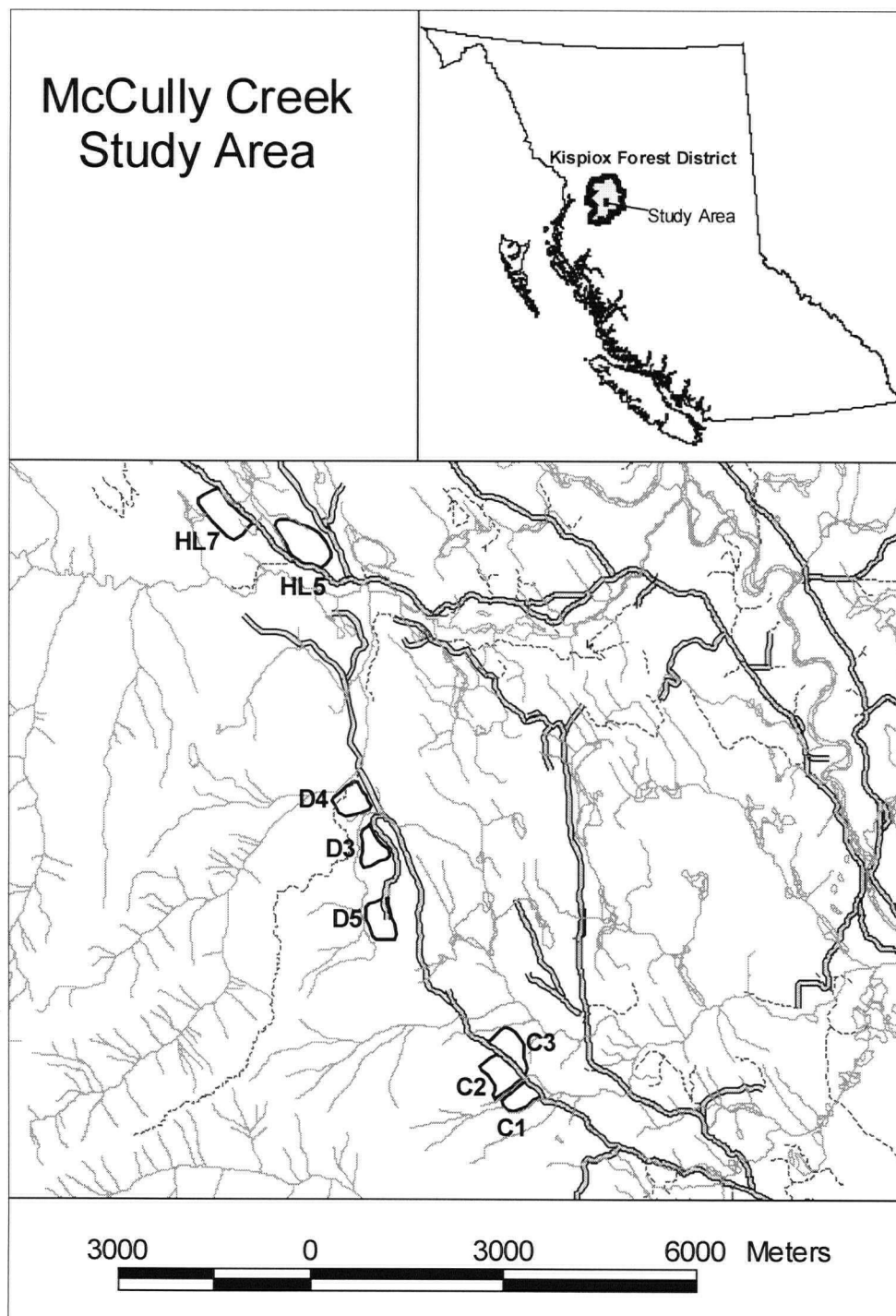


Figure 1.3. Study sites within the McCully Creek study area, British Columbia. Uncut sites = C1, HL7, D3; Partial cut-mature sites = C3, HL5, C2; Partial cut-old sites = D5, D4.

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CHAPTER 2:

NEST SURVIVAL OF CHICKADEES IN MANAGED FORESTS: HABITAT, PREDATOR, AND YEAR EFFECTS¹

INTRODUCTION

Nest predation is the primary cause of nest mortality for songbirds across a wide variety of habitats and geographic locations (Martin 1993a, 1993b). Most studies have documented patterns of nest predation in relation to habitat instead of examining how nest predation is influenced by the autecology, the relationship between species and environmental conditions (Paton 1994, Keyser et al. 1998), or the numerical and functional responses (Chalfoun et al. 2002, Schmidt and Ostfeld 2003a) of predators. If the process of nest predation is an interaction between predator and prey, it is likely influenced by characteristics of the predator, the prey, and the environment (Schmidt 1999). For example, characteristics of the predator may include the density and foraging strategies of the predator, while characteristics of the prey may include selection of nesting habitat to minimize predation. The availability of alternate food for the predator may be a key characteristic influencing nest predation in a particular environment.

The temporary availability of pulsed resources can exert strong influences on predator-prey communities. In New Zealand, stoats (*Mustela erminea*) depredated nestlings of endemic birds after a decrease in the availability of mice and rats (King 1983). Following years of masting beech crops, rodent and stoat densities responded numerically until rodent numbers crashed, and stoats switched from mice and rats to

¹ “A version of this chapter has been accepted for publication. Mahon, C. L., and K. Martin. 2006. Nest survival of chickadees in managed forests: habitat, predator, and year effects. *Journal of Wildlife Management*.”

birds. In temperate deciduous forests, masting acorn crops influenced small mammal populations and nest predation rates on forest songbirds (McShea 2000, Schmidt et al. 2001, Schmidt 2003). The cascading effects of heavy acorn production in the fall (year t) resulted in two negative effects on forest songbirds: nest predation by rodents (year $t + 1$) and predation on fledglings, juveniles, and adults by hawks (year $t + 2$). Hawks responded numerically and functionally to increased rodent densities and then switched to songbirds when the availability of rodent prey decreased (Schmidt and Ostfeld 2003a). Red squirrels (*Tamiasciurus hudsonicus*) primarily consume and cache seeds, but they are also important predators of forest songbirds (Martin 1993a, Sieving and Willson 1998, Tewksbury et al. 1998). The annual abundance of cone crops is related to squirrel population density (C. Smith 1968, M. Smith 1968, Kemp and Keith 1970) and reproductive success (Rusch and Reeder 1978, Wheatley et al. 2002), although there is no evidence that squirrels switch to nests of forest songbirds during periods of low seed availability.

I investigated the effects of habitat and predators at multiple scales because forest type and predator density may influence nest predation at a stand scale, while nest height and proximity to a predator activity area (cache or den site) may influence nest predation at the scale of the nest tree. Nests located in close proximity to high use activity areas may have an increased risk of predation depending on the cues predators use to locate nests (Martin 1993b).

I examined the influence of year, habitat, and predators on chestnut-backed chickadee (*Poecile rufescens*) nest survival across a range of uncut and partial cut stands in northwest British Columbia during 2000-2003. I considered 3 spatial scales of habitat: (1) the stand (19-24 ha of uncut and partial cut stands), (2) the nest patch (a 0.031 ha

patch centered on nest trees), and (3) the nest tree. At each scale I hypothesized that nest survival time of chickadees differed between years, as a result of harvest treatment, habitat characteristics, and predator activity.

STUDY AREA

My study area was within the McCully Creek watershed, approximately 35 km north of the town of Hazelton, British Columbia, Canada, in the Interior Cedar-Hemlock moist cold (ICHmc) biogeoclimatic ecological subzone (see Chapter 1).

I established 3 uncut and 5 partial cut sites (19-24 ha) ranging from low intensity harvest (30% of the stand volume as single trees and small patch cuts) to high intensity harvest (60% of the stand volume with 30% in openings of 0.1 to 0.5 ha and 30% as single trees between openings; Coates et al. 1997). In partial cut sites, trees were removed across all species and diameter classes. Time since harvest for partial cut stands ranged from 3 to 8 years. All study sites were within mature and old forest stands (> 145 years) and contained 50 m x 50 m grid systems.

METHODS

Nest Location and Monitoring

I monitored populations of chestnut-backed chickadees in 6 study sites in 2000 (preliminary year) and 8 study sites from 2001 to 2003. I used modified line transect surveys to locate breeding pairs and the breeding behaviour of adults to locate nests. I used behavioural cues to assess breeding stage and nest fate (boundary disputes with neighbouring pairs, courtship vocalizations and displays, copulation events, nest excavation or renovation, incubation and brooding behaviour) because most nest sites were inaccessible and unstable; I wished to minimize the potential negative impacts of invasive nest monitoring. I marked nests with flagging tape located > 10 m from the nest,

and I monitored nests every 2-3 days until the nest failed or young fledged. Evidence of nest predation included one of the following: an enlarged cavity entrance, nest material pulled out to the cavity entrance, or eggshell or nestling remains at the base of the nest tree. I identified predator species by identifying incisor marks or fresh claw marks around the cavity entrance and hair located on the tree bole near the cavity. I defined nest fate as successful (at least 1 young fledged from the nest) or failed (no young fledged from the nest).

Nest Patch and Tree Habitat Sampling

I recorded vegetation and tree characteristics in 10 m radius circular plots centered on the nest tree during the year the nest was active. I used ocular estimation to assess percent cover of vegetation layers in the nest patch: tree; total shrub; herb; and moss, lichen, and seedling layers. I recorded the habitat type within the nest patch as: uncut forest, thinned forest, harvested gap, and riparian area (small seepage areas, streams). I recorded whether each tree > 12.5 cm was live or dead, measured tree diameter at breast height (DBH), and assessed tree health. I recorded the presence of physical defects and classified a tree as diseased/attacked if I detected stem rot, root disease, butt rot, trunk gall, mistletoe, other fungi, or boring insects. I included in my analyses only those tree health agents with $\geq 10\%$ frequency of occurrence. These included 3 physical defects (broken top, frost crack, brown needles) and 3 disease or insect indicators (conk, blind conk, and beetle infestation). I visually assessed wood condition in the first 2 m of the stem thus, scores for wood condition may not represent the wood condition at the location of nest cavities. I followed the tree mensuration procedures in Field Manual for Describing Terrestrial Ecosystems (BC Ministry of Forests 1998). I used a clinometer to measure the height of nest trees and nest cavities,

and I used a spherical densiometer to measure foliage density (cover) around the nest tree. I recorded nest position (bole, branch, top), cavity type (natural, primary, secondary, unknown), and total number of cavities in the nest tree.

Predator Density, Space Use, Proximity, and Activity

To obtain an index of squirrel density at the stand scale, I conducted squirrel sign surveys during early July in 2001-2003. For each study site I conducted transect surveys along grid lines at 100 m intervals and recorded 6 types of squirrel sign: feeding sign (bracts from single or several cones where squirrels have been feeding), scatter hoards (dispersed, relatively small cone caches), middens (large cone caches), digs (small hole in moss layer from burying cones or searching for fungus), and audio and visual detections. I numbered locations and types of sign and plotted these on study site maps. I classified the age of feeding sign, scatter hoards, middens, and digs as fresh (green cones from current season), recent (bracts not discoloured), or old (bracts decayed, weathered, or covered by debris). I recorded all sign types in a 4 m wide belt, while I recorded audio and visual detections within a 100 m wide belt. I alternated transects surveyed between years to ensure complete coverage of each study site. For each study site, I used the average number of detections/ha for each sign type (mean of all transects) as an index of squirrel density in each year. To assess space use by squirrels, I calculated the proportion of 50 m transect segments containing fresh or recent sign of any type within a study site. The proportion of transect segments containing sign was arcsine transformed, and I used this as the percentage of space used by squirrels in each year.

As a measure of squirrel proximity at the nest patch and nest tree scales, I measured the distance from each chickadee nest detected during 2000 to 2003 to an active squirrel cache site (scatter hoard or midden). To assess the level of squirrel

activity near chickadee nests, I quantified the number of fresh or recent sign within a 100 m radius of each nest (3.14 ha nest area plot). I omitted nests located > 50 m outside study site boundaries because I did not conduct any squirrel sign surveys outside of the study site. I divided the number of sign observations by the distance surveyed within each nest area plot to obtain sign per m, and I used this variable as a measure of squirrel activity within each nest area. I used the squirrel sign data collected on the transects described above, and as a result, the distance surveyed within a nest area varied; average distance surveyed within a nest area was 221 ± 13 ($\bar{x} \pm \text{SE}$) with a range of 68-354 m. Four nest areas with < 57 m of transect within them were excluded from analysis.

Statistical Analyses

For each nest I estimated exposure days from the first day a nest was observed active to the day a nest failed or fledged. For nests with known fate (success or fail), the last exposure day was the midpoint between the last day the nest was checked and the previous visit. For nests with unknown fate, the last exposure day was the last day the nest was known to be active (last active date). These procedures generally result in the least bias (Manolis et al. 2000). I calculated daily mortality rate (DMR) by dividing the number of failed nests by the total number of nest exposure days (Mayfield 1975), and I calculated predator daily mortality rate (PDMR) by dividing the number of nests destroyed by a predator by the number of nest exposure days. From the PDMR I calculated the proportion of nests depredated (when extrapolating the PDMR to a 33 day nesting cycle) as: $(1 - \text{PDMR})^d$, where d is the number of days in the nesting cycle (incubation and nestling period) of chestnut-backed chickadees (Schmidt and Ostfeld

2003a). For calculations of apparent nest failure and daily nest mortality, I included all active nests detected during 2000 to 2003 ($n = 69$).

I used logistic regression to predict nest outcome (successful vs. depredated) from habitat characteristics at the patch and the nest tree scales because no prior studies of natural nest sites exist for this species. I included all successful nests and all failed nests that were known to be depredated during 2000-2003 ($n = 57$). I first conducted logistic regression on each habitat variable (13 nest patch and 17 nest tree variables). I used 2 criteria to assess models: (1) the statistical significance of the coefficient and (2) the goodness of fit or χ^2 test = $2[(\log\text{-likelihood for full model}) - (\log\text{-likelihood for constant-only model})]$. I included all nest patch and nest tree variables that were significant in the analyses at $P < 0.25$ in an initial multivariate logistic model (full model). I used 2 methods to evaluate the contribution of an individual predictor variable to a model; I used the Wald test to evaluate whether the coefficient differed from 0, while I used the likelihood-ratio test to compare the model with and without the predictor being tested (Tabachnick and Fidell 2001).

I used an information-theoretic approach to determine support for models representing alternative hypotheses for differences in nest survival time due to year, habitat, and predator effects. I developed sets of candidate models at each of 3 scales: (1) the stand, represented by 19-24 ha of uncut and partial cut study sites; (2) the nest patch, represented by a 0.03 ha forest patch centered on nest trees; and (3) the nest tree. I used harvest treatment (uncut or partial cut) as a stand scale habitat variable. I used the logistic regressions developed to predict nest outcomes to also select nest patch and nest tree scale habitat variables. Predator variables included an index of squirrel density (number of feeding sign detections [age = recent]/ha) at the stand scale and squirrel

proximity at the nest patch and nest tree scales. I included the variable year as a categorical variable in all models because apparent nest failure and daily nest mortality data exhibited strong year effects. By comparing models with and without the habitat effect, I determined support for the hypotheses that nest survival differed (1) between harvest treatments (uncut and partial cut stands) and (2) with habitat characteristics at the nest patch and nest tree scales. By comparing models with and without the predator effect, I determined support for the hypotheses that nest survival differed with predator density and predator proximity. To examine the effect of harvest treatment at the nest patch and nest tree scales, I also included harvest treatment in the nest patch and nest tree sets of candidate models.

I used Cox regression or Cox proportional-hazards regression (SPSS COXREG) to estimate the survival models. This approach models event (failure) rates as a log-linear function of continuous or categorical predictor variables, called covariates. Regression coefficients give the relative effect of each covariate on the survivor function (Tabachnick and Fidell 2001). Cox regression allows censored observations to be included in the analysis (successful and uncertain nests), and it uses a continuous response variable (nest age or time to failure). Nest age or nest survival time may be a more appropriate response variable than nest fate (i.e., logistic regression) because the former considers the length of time nests are observed (Manolis et al. 2000). I terminated nest survival times in the same manner as described for calculating exposure days and only included nests that reached the start of incubation during 2000-2003 ($n = 63$). I included 7 observations of nest reuse because the proportion of nesting attempts by birds nesting in the same cavity was low ($7/63 = 11\%$). To evaluate individual Cox regression survival models, I examined the likelihood ratio test, regression coefficients, and odds

ratios or the odds of surviving (a positive regression coefficient and odds ratio > 1 indicates an increased likelihood of nest failure). The overall risk score for survival time is comprised of the regression coefficients for each significant covariate. To examine the influence of harvest treatment at the nest patch and nest tree scales, I examined the change in the likelihood ratio test with the addition of harvest treatment as a predictor. I tested the assumption that the hazard or risk ratio was proportional over time by examining interactions between a time variable (natural logarithm of time) and each covariate. None of the covariates significantly interacted with time (all P values > 0.04) at $\alpha = 0.017$ (3 covariates at each scale; Tabachnick and Fidell 2001). I calculated Akaike's Information Criteria for small sample sizes (AIC_c), ΔAIC_c , and I calculated Akaike weights (w) to identify the best models at each spatial scale (Burnham and Anderson 1998).

I used a one-way ANOVA (General Linear Models) to examine differences among years and between treatments for DMR and PDMR, and a one-way ANOVA to examine differences among years for squirrel density, squirrel space use, and squirrel activity in nest areas. I used the Kruskal-Wallis test to compare squirrel proximity between years. I examined relationships between stand scale predator variables (squirrel density, space use) and DMR in each year using linear regression. At the nest patch and nest tree scales, I examined relationships between squirrel proximity or squirrel activity and nest survival time in each year using linear regression. I used SPSS 11.0 (SPSS Inc. 2001) in all analyses performed.

RESULTS

During 2000 to 2003, I documented 69 chestnut-backed chickadee nesting attempts in 61 natural cavities, of which 34 (49%) were successful, 33 (48%) failed, and

2 (3%) had uncertain outcomes. Of the 33 nests that failed, 23 (70%) were depredated while 10 (30%) were abandoned, possibly due to adult mortality or inclement weather. Eight of 69 nesting attempts (12%) were in previously used cavities (2 cavities used for 3 years, 4 used for 2 years). Cavity reuse was not linked to a successful nesting attempt in a previous year as 4 of 6 cases of nest reuse occurred after a failed nesting attempt. Overall nest failure was highest in 2001 at 82% and lowest in 2002 at 24%, with predators accounting for 64% of nest losses in 2001 and 9.5% in 2002. Chickadee nest mortality rates and predator mortality rates were high in 2000 and 2001 ($> 57\%$ of nests depredated when extrapolating the PDMR to a 33-day nesting cycle), whereas mortality and predator mortality rates were low in 2002 and 2003 (Table 2.1). There was no difference among years for DMR ($F_{3,4} = 5.12$, $P = 0.11$), or PDMR ($F_{3,4} = 5.08$, $P = 0.11$) or between uncut and partial cut study sites for DMR ($F_{1,6} = 0.70$, $P = 0.46$) and PDMR ($F_{1,6} = 0.36$, $P = 0.59$).

Squirrels were the primary nest predators. Incisor marks around the cavity entrance of 74% of 23 depredated nests identified either the red squirrel or northern flying squirrel (*Glaucomys sabrinus*) as the predator. I could not distinguish squirrel hair that I found at the cavity entrance of depredated nests from squirrel fur used to line chickadee nest cavities. Intensive live trapping for squirrels resulted in captures of only red squirrels within this study area (J. D. Steventon, Ministry of Forests, personal communication). I observed red squirrels preying on nestlings in 4 nests and using parental activity as a cue to finding nests (Martin and Li 1992; C. L. Mahon, personal observation). I found claw marks below the depredated nest cavity and dorsal hair of a marten (*Martes americana*) at 1 nest.

Nest Patch and Nest Tree Habitat

To examine relationships between nest success and nest patch habitat, I pooled data from all study sites and years. At the nest patch level, 6 habitat variables were related to nest success in the logistic regression analysis at $P < 0.25$ (Appendix I). The odds of a successful nest was: 0.11 times as likely with a 1 unit increase in high shrub cover, 0.15 times as likely with an increase in beetle-infested trees, 0.78 times as likely with an increase in broken top trees, and 0.89 times as likely with an increase in frost crack trees. Nest patch habitat type also influenced nest success, although no specific habitat category reliably predicted nest success (Appendix I). Only habitat type emerged as a reliable predictor of nest success in the multivariate logistic regression analysis. The model with habitat type did not differ from a constant-only model ($\chi^2 = 8.58$, $df = 5$, $P = 0.13$), but the model with habitat type omitted was different from the full model ($G^2 = 8.04$, $df = 3$, $P = 0.004$), indicating that the inclusion of habitat type improved the fit of the full model.

I pooled nest tree habitat variables from all study sites and years and divided these into tree and nest placement categories as part of a study of chestnut-backed chickadee nest site selection reported elsewhere (Chapter 3). Five variables were predictors of nest success in the logistic regression analysis at $P < 0.25$; 3 tree variables (tree species, disease, blind conks) and 2 nest placement variables (nest height and nest tree cover, Appendix I). Because the variables disease and blind conks were correlated, I entered each variable into a separate logistic regression model with the other predictor variable (tree species). I found that a test of the model with tree species and disease against a constant-only model was not statistically reliable ($\chi^2 = 14.04$, $df = 8$, $P = 0.08$), indicating that the set of predictor variables did not distinguish between successful and depredated

nests. Similarly, the model with tree species and blind conks did not differ from a constant-only model ($\chi^2 = 14.63$, $df = 8$, $P = 0.07$). The model with nest tree cover and nest height did differ from a constant-only model ($\chi^2 = 9.93$, $df = 2$, $P = 0.007$); both nest height and nest cover were predictors of nest success. The model with nest height omitted was different from the full model ($G^2 = 8.16$, $df = 1$, $P = 0.004$), suggesting that the inclusion of nest height improved the fit of the full model. In a similar test, a model with nest tree cover omitted also differed from the full model ($G^2 = 4.74$, $df = 1$, $P = 0.03$). Because nest tree cover had a small influence on nest success (odds ratio = 0.001, CI: 0.00 to 0.830), I selected nest height as the nest tree scale variable (odds ratio = 1.11, CI: 1.01 to 1.22). With a 1 unit increase in nest height and nest tree cover, the odds of a successful nest was 1.1 times as likely (odds increased by 10%).

Nest Survival

Based on model selection results, I used the model containing year to predict nest survival time of chestnut-backed chickadee nests at the stand scale ($\chi^2 = 17.15$, $df = 2$, $P < 0.001$). The AIC-selected model had a weight of 0.565, while the second-best model had a weight of only 0.190 (Table 2.2). Only the variable year predicted nest survival time at $\alpha = 0.025$: Risk = 1.82 (Year 2001). The risk score for survival time was comprised of the regression coefficients for each significant covariate. There was no effect of harvest treatment after adjusting for year and predator density ($G^2 = 0.01$, $df = 1$, $P = 0.91$).

At the nest patch scale, I found support for the models year and year, predator proximity (Table 2.3). I found no effect of harvest treatment at the nest patch level ($G^2 = 0.02$, $df = 1$, $P = 0.88$ for year, habitat-patch; $G^2 = 0.12$, $df = 1$, $P = 0.73$ for year, predator proximity; $G^2 = 0.11$, $df = 1$, $P = 0.75$ for year, habitat-patch, predator

proximity). I selected the model containing year because it was the only covariate that predicted nest survival time ($\chi^2 = 18.27$, $df = 3$, $P < 0.001$): Risk = 1.81 (Year 2001). Stand and nest patch scale models suggested that for a chickadee nesting in 2001, the odds of nest failure increased more than 6 times.

At the nest tree scale, I found support for the models year, habitat-nest and year, habitat-nest, predator proximity (Table 2.4). I found no effect of harvest treatment at the nest tree level ($G^2 = 0.04$, $df = 1$, $P = 0.84$ for year, habitat-nest; $G^2 = 0.02$, $df = 1$, $P = 0.88$ for year, habitat-nest, predator proximity). Although some model selection uncertainty existed, nest height appeared in both of the top 2 models, and only the model with year and nest height had individual covariates that predicted survival time. I selected the model with year and nest height to estimate survival time ($\chi^2 = 21.17$, $df = 4$, $P < 0.001$): Risk = 1.67 (Year 2001) - 0.08 (Nest Height). At $\alpha = 0.0125$, only the covariate year predicted survival time ($B = 1.67$, $P = 0.009$), although nest height also contributed to the model outcome ($B = -0.075$, $P = 0.03$). The odds of nest failure for chickadees increased by 5.3 times in 2001 over other years, although a 1 metre increase in nest height decreased the odds of nest failure by 7% (odds ratio = 0.93, CI: 0.86 to 0.99).

Predator-year Effects

To examine if the pronounced year effects influenced predator variables, I first compared stand scale predator variables (index of squirrel density, space use) and nest patch/nest tree variables (squirrel proximity, squirrel activity at nest areas) between years. At the stand scale, I found no annual differences in the index of squirrel density ($F_{2,21} = 1.51$, $P = 0.25$) or in squirrel space use ($F_{2,21} = 0.74$, $P = 0.50$). At the scale of the nest patch/nest tree, I found that distance to a squirrel cache site (squirrel proximity) differed

annually ($\chi^2 = 10.52$, $df = 2$, $P = 0.005$; 2001-18.61 m, 2002-34.42 m, 2003-25.21 m), while squirrel activity at nest areas did not differ ($F_{2,48} = 0.62$, $P = 0.54$). Small sample sizes prevented an examination of year x study site interactions. I found no relationship between my squirrel density index or squirrel space use and daily mortality rate (DMR) in any year (all P values > 0.05). I found no relationship between squirrel proximity or squirrel activity in nest areas and nest survival time in any year (all P values > 0.05).

DISCUSSION

Strong and weak primary excavators reportedly suffer lower rates of nest predation than nonexcavators (secondary cavity nesters like wrens and bluebirds) and open-cup nesters (Martin and Li 1992; but see Nilsson 1986). Rates of nest failure for chestnut-backed chickadees were higher than the range reported for other conifer-associated weak primary excavators (Martin and Li 1992, Hailman and Haftorn 1995, Ficken et al. 1996). Further, I observed dramatic annual variation in chestnut-backed chickadee nest failure ranging from 24% to 82%, which was unrelated to harvest treatment. I suggest that annual variation in chickadee nest survival resulted from changes in food availability for red squirrels, the dominant predator.

I observed red squirrels gain access to chestnut-backed chickadee nests by using their incisors to enlarge the cavity entrance. Previous studies done during the breeding season may have underestimated rates of nest predation by using nest boxes (Copper et al. 1978, Gold and Dahlsten 1983, Kleintjes and Dahlsten 1994, Brennan et al. 2000). Cavities may offer less protection for weak primary excavators like chickadees because they are located in sections of the tree containing soft, rotting wood. In comparison, strong primary excavators like the pileated woodpecker (*Dryocopus pileatus*) and the hairy woodpecker (*Picoides villosus*) can excavate cavities in live or dead trees with

decayed heartwood surrounded by sound sapwood (Harestad and Keisker 1989, Martin et al. 2004). None of the nests of strong primary excavators like red-breasted sapsuckers (*Sphyrapicus ruber*), three-toed woodpeckers (*Picoides tridactylus*), and hairy woodpeckers I monitored were depredated by squirrels (C. L. Mahon, unpublished data). Chestnut-backed chickadees nesting in cavities ($n = 69$) suffered 48% nest failure (this study) but only 38% nest failure in nest boxes in California ($n = 237$), with 8% of mortality due to nest predation and 27% of mortality due to abandonment (Dahlsten et al. 2002). In natural nests, the closely related boreal chickadee (*Poecile hudsonicus*) and Siberian tit (*Parus cinctus*) had failure rates of 18% (McLaren 1973) and 30-40% (Järvinen 1982; 1990), respectively. Chickadees found in conifer and mixed forests had nest failure rates of 39% for the mountain chickadee (*P. gambeli*; Martin and Li 1992) and 34% for the Carolina chickadee (*P. carolinensis*; Albano 1992). Thus nest failure for chickadees usually varies from 30 to 48%, only slightly lower than failure rates for many open cup nesters (Martin 1993b).

Vegetation structure has been considered a key factor influencing predation rates on nests (Li and Martin 1991, Martin 1993a, Easton and Martin 2002). However, harvest treatment, nest patch, and nest tree variables did not influence the nest survival of chestnut-backed chickadees. Partial cutting did not appear to negatively impact the availability of suitable nest sites for chickadee pairs, as I found no relationship between the density of pairs and the density of trees, dead trees, or diseased trees (Chapter 3). Nest patch and nest tree vegetation variables may have had little influence on nest survival if yearly fluctuations in predation risk, rather than habitat characteristics, determined patterns of nest predation.

Only nest height, a nest placement variable, was a reliable predictor of nest survival in the nest tree model. Although higher nest cavities may suffer less predation in some systems (Li and Martin 1991), predator responses to nest height may be species-specific (Walters and Miller 2001). In conifer and mixed forests, the red squirrel was the dominant predator of forest songbirds in studies of artificial nests (Martin 1988, Bayne and Hobson 1997, Darveau et al. 1997) and natural nests (Martin 1993a, Sieving and Willson 1998, Tewksbury et al. 1998, this study). In my study area, artificial nest experiments using quail and plasticene eggs identified the red squirrel as the dominant predator of cup nests (Steventon et al. 1999). Only 1 artificial cavity nest was depredated by a small mammal (mouse) predator (C. L. Mahon, unpublished data). Red squirrels spend time on the ground (visiting cache sites) and in trees (visiting nest sites, foraging), and therefore may detect nesting chickadees from many vantage points. A nest cavity higher in a tree may be more difficult for a squirrel to detect because the sounds of vocalizing adults or begging nestlings may be obscured, and crown foliage may screen the nest cavity. In other studies, cavity-wall thickness (Christman and Dhondt 1997, Wiebe 2001), wood hardness (Harestad and Keisker 1989, Albano 1992, Dobkin et al. 1995), and nest entrance size and shape (Nilsson 1984, Martin et al. 2004) were important factors influencing nest site selection of weak cavity nesters. Wood condition could be important in my system because harder wood could restrict access to a nest cavity by a red squirrel. As the average nest height was 11.4 m, I could not assess wood condition for most of my chickadee nest cavities.

A number of studies have suggested that predator density (Schmidt et al. 2001, Schmidt 2003, Schmidt and Ostfeld 2003a), space use (Schmidt and Ostfeld 2003b), and activity (Pelech 1999, Chalfoun et al. 2002, Cain et al. 2003) may affect nest predation

rates of forest songbirds. I found no relationship between chickadee nest mortality and red squirrel density and space use at the stand scale, or cache site proximity and nest area activity at the nest patch/nest tree scale. While my predator activity measures may have been too imprecise to detect changes in numbers of squirrels between years, density may not be the only factor influencing nest predation rates. Information on the foraging patterns (prey diversity, prey switching) and foraging behaviour of specific predators and in particular, how they find nests (e.g., opportunistic, directed search), is needed to understand predator-prey relationships. Additionally, red squirrels with nest finding experience may locate and prey on more nests than less experienced squirrels (Pelech 1999). Spatial memory, which is likely used by red squirrels to relocate productive food patches or cache sites, may be used to locate previous nest locations.

Red squirrels, as generalist consumers, can forage on a wide variety of food items including seeds, buds, catkins, fruits, fungi, insects, mice, bird eggs and nestlings (Banfield 1974), chipmunks and other tree squirrels (Callahan 1993), and juvenile snowshoe hare (O'Donoghue 1991). In diverse forest types like the ICH, red squirrels may consume a variety of food items that differ in their resource quality and availability, including seeds from conifer cones (high resource quality, unstable availability), and fungi, fruit, and buds (low resource quality, stable availability). I suggest that annual variation in nest predation rates may be due to changes in resource availability that alters red squirrel habitat quality. Squirrels store their main food supply, the seeds of conifer cones, in small scatter hoards, large larder hoards, or middens within a defended territory (Hurley and Lourie 1997). The composition and abundance of mast seeding conifer species within forest habitats results in differences in seed availability over time and space (Koenig and Knops 2000). The availability of these preferred food items may regulate

red squirrel populations. For example, white spruce forests appear to support red squirrel populations with high, stable densities, low mortality rates, and high reproductive rates (M. Smith 1968, Kemp and Keith 1970, Rusch and Reeder 1978). However, in a study examining the effects of habitat-specific resource fluctuation, red squirrel demography was similar in white spruce, mixed conifer, and lodgepole pine habitats 1 year after a spruce-cone failure, suggesting that squirrel populations tracked conifer seed availability (Wheatley et al. 2002).

Although I attempted to measure food availability for squirrels within my study sites, 3 characteristics of my system limited data collection: (1) large number of tree species (5 conifer and 3 deciduous species), (2) scattered distribution of secondary tree species within stands, and (3) wide diversity of food items consumed by squirrels (seeds of 6 tree species, catkins, buds, fungi, berries). Measuring cone or seed availability for all tree species is needed because the presence of multiple masting species within forest stands could result in synchronous or asynchronous mast events. Synchronous events may magnify the total size of seed crops in mast years and result in very low seed crops in mast failure years, while asynchronous events may result in a stable seed supply (Schmidt 2003). Since I observed no difference in squirrel density or space use between years, it is possible that a large mast failure in the fall of 1999 and 2000 may have severely limited seed availability for red squirrels causing them to prey on high numbers of chickadee nests during the 2000 and 2001 breeding seasons. If high quality seeds became available to squirrels during the fall of 2001, and were cached and consumed over the following year, lower rates of nest predation would have resulted in 2002. I suggest that red squirrels may have exhibited a functional response, shifting from food

items consumed following low mast years (bird eggs and nestlings) to preferred items consumed following high mast years (high quality conifer seeds).

MANAGEMENT IMPLICATIONS

Managers and researchers need to consider the influence of ecological factors in addition to habitat characteristics and predator density or activity on the nest success of forest songbirds. Strong annual variation in rates of nest predation, which are commonly observed for avian populations in most temperate systems, suggest the need to examine how temporal variation in resource availability influences predators. We recommend conducting multi-year studies and documenting responses of predators (numerical, functional) to changes in (1) primary and alternate food sources, and (2) habitat structure to help predict annual variation in songbird nest survival.

Table 2.1. Daily mortality rates (DMR) and predator daily mortality rates (PDMR) for chestnut-backed chickadees nesting in uncut (UC) and partial cut (PC) stands at McCully Creek, British Columbia, 2000-2003.

| | 2000 | | 2001 | | 2002 | | 2003 | |
|-----------------------------------|-------|-------|-------|-------|------|-------|-------|-------|
| | UC | PC | UC | PC | UC | PC | UC | PC |
| DMR | 0.061 | 0.028 | 0.035 | 0.034 | 0 | 0.005 | 0.011 | 0.011 |
| PDMR | 0.061 | 0.028 | 0.025 | 0.028 | 0 | 0.003 | 0 | 0.005 |
| Nests depredated (%) ^a | 87.5 | 60.8 | 56.6 | 60.8 | 0 | 9.4 | 0 | 15.2 |
| <i>n</i> ^b | 3 | 6 | 8 | 14 | 6 | 15 | 4 | 13 |

^aI calculated the percentage of nests depredated as $[1 - (1 - \text{PDMR})^d] \times 100\%$, where *d* is the number of days in the nesting cycle. For calculations, chestnut-backed chickadee *d*=33.

^b*n* was the number of nests.

Table 2.2. Cox regression models for stand scale effects of year, habitat, and predators on survival of chestnut-backed chickadee nests in McCully Creek, British Columbia, 2001-2003. Models are ranked from best to worst based on Akaike's Information Criteria for small sample sizes (AIC_C), delta (ΔAIC_C), and Akaike weights (w); AIC_C is based on $-2 \times \log$ likelihood (L), the number of parameters in the model (K), and sample size (n).

| Model | $-2 (L)$ | K | AIC_C | ΔAIC_C | w |
|--|----------|-----|---------|----------------|-------|
| Year | 140.29 | 2 | 144.52 | 0 | 0.565 |
| Year, predator density ^a | 140.23 | 3 | 146.71 | 2.18 | 0.190 |
| Year, habitat-treat | 140.28 | 3 | 146.76 | 2.23 | 0.185 |
| Year, predator density, habitat-treat ^b | 140.21 | 4 | 149.03 | 4.51 | 0.059 |

^aSign/ha was an index of predator density.

^bHabitat-treat was harvest treatment: uncut, partial cut.

Table 2.3. Cox regression models for nest patch scale effects of year, habitat, and predators on survival of chestnut-backed chickadees in McCully Creek, British Columbia, 2000-2003. Models are ranked from best to worst based on Akaike's Information Criteria for small sample sizes (AIC_C), delta (ΔAIC_C), and Akaike weights (w); AIC_C is based on $-2 \times \log \text{likelihood} (L)$, the number of parameters in the model (K), and sample size (n).

| Model | $-2 (L)$ | K | AIC_C | ΔAIC_C | w |
|--|----------|-----|---------|----------------|-------|
| Year, predator proximity ^a | 181.06 | 4 | 189.79 | 0 | 0.425 |
| Year | 183.61 | 3 | 190.02 | 0.23 | 0.379 |
| Year, predator proximity, habitat-treat | 180.94 | 5 | 192.05 | 2.26 | 0.137 |
| Year, habitat-patch ^b predator proximity | 179.25 | 7 | 195.41 | 5.62 | 0.025 |
| Year, habitat-patch | 182.35 | 6 | 195.85 | 6.06 | 0.020 |
| Year, habitat-patch, predator proximity, habitat-treat | 179.15 | 8 | 197.97 | 8.18 | 0.007 |
| Year, habitat-patch, habitat-treat | 182.33 | 7 | 198.37 | 8.58 | 0.006 |

^aDistance to nearest red squirrel cache site.

^bHabitat-patch was habitat type: forest, thinned forest, harvest gap, riparian.

Table 2.4. Cox regression models for nest tree scale effects of year, habitat, and predators on survival of chestnut-backed chickadees in McCully Creek, British Columbia, 2000-2003. Models are ranked from best to worst based on Akaike's Information Criteria for small sample sizes (AIC_C), delta (ΔAIC_C), and Akaike weights (w); AIC_C is based on $-2 \times \log \text{likelihood } (L)$, the number of parameters in the model (K), and sample size (n).

| Model | - 2 (L) | K | AIC_C | ΔAIC_C | w |
|--|-------------|---|---------|----------------|-------|
| Year, habitat-nest ^a , predator | | | | | |
| proximity | 161.66 | 5 | 172.81 | 0 | 0.426 |
| Year, habitat-nest | 164.53 | 4 | 173.25 | 0.43 | 0.343 |
| Year, habitat-nest, predator | | | | | |
| proximity, habitat-treat | 161.64 | 6 | 175.28 | 2.47 | 0.124 |
| Year, habitat-nest, habitat-treat | 164.49 | 5 | 175.58 | 2.77 | 0.106 |
| Year | 183.61 | 3 | 190.02 | 17.20 | 0.000 |

^aHabitat-nest was nest height.

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CHAPTER 3:

HABITAT ATTRIBUTES AND CHESTNUT-BACKED CHICKADEE NEST SITE SELECTION IN UNCUT AND PARTIAL CUT FORESTS¹

INTRODUCTION

Nest site limitation may be important in managed forests where suitable wildlife trees (dying or dead trees) are often removed to meet safety requirements for forest workers (Zarnowitz and Manuwal 1985, Hunter 1990, Steeger and Hitchcock 1998). Cavity nester populations that nest in dead trees may be limited by the availability of suitable nest sites (Brawn and Balda 1988, Newton 1994, Dobkin et al. 1995). Secondary cavity nesters may be particularly vulnerable to the removal of nest sites because they cannot excavate their own cavities (Brawn 1988, Brawn and Balda 1988, Holt and Martin 1997). Chestnut-backed chickadees (*Poecile rufescens*) are found in humid coastal and interior forests and can excavate nest cavities in trees with soft heartwood or renovate existing natural or previously excavated cavities (Dahlsten et al. 2002). Like other weak cavity excavators, chestnut-backed chickadees require decaying wood found in diseased, damaged, or dead trees. The availability of high-quality cavities for chickadees and other cavity nesters within a stand may depend on natural and human-caused alteration of habitat, competition for cavities, and the location of suitable cavities or potential sites for cavities within a stand (Nilsson 1984, Aitken et al. 2002, Aitken and Martin 2004).

Partial cutting has been used to retain structural attributes of natural forests by simulating small-scale patterns of disturbance. In Interior Cedar-Hemlock forests, the

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relative abundance of cavity or bark nesting species like the chestnut-backed chickadee, red-breasted nuthatch (*Sitta canadensis*), brown creeper (*Certhia americana*), hairy woodpecker (*Picoides villosus*), and three-toed woodpecker (*Picoides tridactylus*) was similar in uncut and partial cut forests with 30% and 60% volume removal (Steventon et al. 1998). In Douglas-fir (*Pseudotsuga menziesii*) forests, chestnut-backed chickadees, red-breasted nuthatches, and brown creepers, used small patch group selection stands (30% of volume removed in small circular patterns), two-story stands (75% volume removed with scattered green trees), and modified clearcut stands, but at lower densities than uncut controls. Only chestnut-backed chickadees nested in each of the 3 harvest treatments (Chambers et al. 1999). In high-elevation conifer forests, detections of another weak cavity excavator, the red-breasted nuthatch, did not differ between uncut reserves and a variety of harvest treatments removing 30% volume including single-tree removal, 0.1 ha openings, 1.0 ha openings, and a 10 ha opening, suggesting resistance to small-scale harvesting (Leupin et al. 2004).

In northwest British Columbia during the breeding season, chestnut-backed chickadees occupy conifer-dominated forests that contain live, healthy trees for foraging and diseased, damaged, or dead trees for nesting. Within territories, the area directly surrounding the nest tree (nest patch) can reduce predation risk by providing cover and increasing the number of potential nest sites to be searched by a predator (Martin 1993). In addition, high tree density within the nest patch may increase the availability of proximate foraging substrates (Li and Martin 1991). Nest trees selected by weak cavity excavators can be characterized by the presence of disease, physical defects, and other mortality agents (Harestad and Keisker 1989, Christman and Dhondt 1997, Martin et al. 2004).

How changes in forest structure influence the availability, use, and selection of habitat by forest-dependent wildlife species can be examined by documenting patterns of selection when resource availability changes. In this study, my objectives were to: (1) describe and compare the characteristics of uncut sites to structurally modified partial cut sites, and (2) compare use and selection of chestnut-backed chickadee nesting habitat in uncut, partial cut-mature, and partial cut-old sites at 3 spatial scales: the stand (19-24 ha uncut and partial cut stands), the nest patch (a 0.031 ha patch centered on nest trees), and the nest tree. I used a multiscale approach that includes the range of spatial scales (stand, nest patch, nest tree) over which chickadees are likely to respond to changes in resource availability and habitat heterogeneity.

I assessed habitat use at the stand scale by examining correlations between stand characteristics and breeding population densities. I examined selection at the nest patch and nest tree scales by comparing used resources (nest patch and nest tree attributes) to available resources within chickadee territories (Johnson 1980, Manly et al. 2002). At the nest patch scale, I compared nest plots to plots within the territory of the nesting chickadee pair. At the tree scale, I compared nest trees to (1) trees within nest plots, and (2) trees within territory plots.

Stand age may be an important characteristic for weak cavity nesters like chickadees because older forests are more structurally diverse and have a higher incidence of disease and damage. I predicted higher chickadee densities in mature and old uncut sites and old partial cut sites with high levels of tree retention because chestnut-backed chickadees require both live and dying or dead trees to meet their breeding requirements. I expected to find the lowest availability of suitable nest sites in partial cut-mature sites, and find chickadees using a narrow range of nest sites relative to uncut

and partial cut-old sites because large, diseased, damaged, or dead trees are less abundant.

STUDY AREA

My study area was within the McCully Creek watershed, approximately 35 km north of the town of Hazelton, British Columbia, Canada, in the Interior Cedar-Hemlock moist cold (ICHmc) biogeoclimatic ecological subzone (see Chapter 1).

I established 3 uncut and 5 partial cut sites (19-24 ha) ranging from low intensity harvest (30% of the stand volume as single trees and small patch cuts) to high intensity harvest (60% of the stand volume with 30% in openings of 0.1 to 0.5 ha and 30% as single trees between openings; Coates et al. 1997). In partial cut sites, trees were removed across all species and diameter classes. Time since harvest for partial cut stands ranged from 3 to 8 years. All study sites were within mature and old forest stands (> 145 years) and contained 50 m x 50 m grid systems.

METHODS

Chickadee Breeding Density and Nest Location

I monitored chestnut-backed chickadee pairs in 6 sites in 2000 (preliminary year) and 8 sites from 2001 to 2003. From early May to mid-June in each year, modified line transect surveys were used to locate breeding pairs. I then followed chickadees and recorded location, number of individuals, and behaviour on 1:4000 scale site maps referenced to a 50 m grid in the field. Each pair of observers monitored 4 sites for the entire nesting season by surveying the site and then searching "hot spots" on alternate days (Martin and Geupel 1993). I calculated the average breeding pair density using territories or pairs from 2001 to 2003. Density was based on the total number of breeding pairs with complete or partial territories within sites and included all known pairs found

within sites, not just pairs with sufficient data to calculate a home range estimate (20-30 location points). I determined territory boundaries by plotting locations obtained from (1) conducting line transect surveys, and (2) following birds exhibiting territorial behaviour (Bibby et al. 2000). I estimated the territory size for complete and partial territories within the site and assigned 1 of 4 size categories to each territory: 1 = complete territory, and 0.75, 0.50, and 0.25 = partial territory. I chose the site containing the largest portion of the territory when territories occupied more than 1 site. I observed pairs using 2 adjacent sites (up to 2 pairs in any year). One pair crossed a road (50 m total width) to use habitats from 2 sites. Nests were located by observing the breeding behaviour of adult birds (boundary disputes with neighbouring pairs, courtship vocalizations and displays, copulation events, nest excavation or renovation, incubation and brooding behaviour), marked with flagging tape located > 10 m from the nest, and monitored every 2 to 3 days until the nest failed or young fledged.

Habitat Sampling

I assessed vegetation characteristics within circular plots of 10 m radius (0.031 ha) centered at all active nest trees (nest plot), at a close plot (the nearest grid point location to the active nest), and a random plot. To characterize available habitat and describe forest structure at the stand scale, each uncut and partial cut site was divided into 4 quadrants from which a random plot was selected. I established 8-12 random plots per site (approximately 1.6-2.5/ha). To describe habitat within the nest patch and available habitat within a chickadee territory of each pair with an active nest, I established nest plots and close plots. Within all plots I counted the number of pole-sapling trees, visually estimated percent cover of tree, total shrub, herb, and moss/lichen/seedling vegetation layers, and recorded habitat type: uncut forest, thinned forest, harvested gap, and riparian

area (small seepage areas, streams, wetlands). Random plots were sampled from 2000 to 2002, and nest and close plots from 2000 to 2003.

For each tree (> 12.5 cm diameter) within all plots I recorded tree species, DBH (diameter at breast height of 1.3 m above ground), whether the tree was alive or dead, tree condition, wood condition, and tree health using tree mensuration procedures developed for collecting ecological data in British Columbia (BC Ministry of Forests 1998). Tree condition was assessed using the shape of the tree stem and the state of the crown. I assessed wood condition in the first two m of the stem and as a result, scores for wood condition may not represent the wood condition at the location of nest cavities. To assess tree health, the presence of various health agents (disease, insects, physical defects) was recorded. A tree was classified as diseased/attacked if I detected the presence of any disease or insects (stem rot, root disease, butt rot, trunk gall, mistletoe, other fungus, boring insects). I used pathological indicators such as fungal fruiting bodies (conks) and blind conks (decay associated with knots or branch stubs) to infer stem rot, mycelial fans and resinosis to infer root disease, wood condition to infer butt rot, and excessive branching (witches' brooms) or abnormal swelling to infer the presence of dwarf mistletoe (*Arceuthobium*). Low levels or early stages of fungal and mistletoe infections could not be detected using these methods. I used the presence of exit holes, galleries, and pitch tubes to determine if a tree had boring insects. Although trees were assessed using 18 specific health agents, I included in my analyses only those health agents with $\geq 10\%$ frequency of occurrence in all 1961 trees surveyed in the random plots. These included 3 disease or insect indicators (conk, blind conk, and boring insects) and 3 physical defects (broken top, frost crack, brown needles).

At nest trees I used a clinometer to measure tree and cavity height and a spherical densiometer to measure foliage density (cover) around the tree. I also recorded nest position (bole, branch, top), cavity type (natural, primary, secondary, unknown), and total number of cavities in the nest tree. I measured nest tree characteristics during the year a nest was active.

Within all random plots (stand scale) and nest and close plots (nest patch scale), I summarized the density of vegetation characteristics (density of trees, density of pole-sapling trees, percent cover) per plot (0.031 ha sampling plot).

Using this sampling scheme I characterized habitat availability and use by chestnut-backed chickadees at 3 scales. At the stand scale I described available habitat in uncut and partial cut sites and examined patterns of use by relating breeding density to stand scale characteristics. At the nest patch scale, I compared nest plots to plots within the territory of the nesting chickadee pair (close plot). At the tree scale, I compared nest trees to (1) trees within nest plots, and (2) trees within close plots.

Statistical Analyses

All analyses were performed using SPSS 11.0 (SPSS Inc. 2001). I used nesting data (nest patch and nest tree scales) and vegetation data collected during 2000-2003. I used breeding density data (stand scale) collected during 2001-2003 because we were unable to collect detailed breeding population densities in 2000. Percent cover variables for each vegetation layer were arcsine transformed prior to analysis of variance (ANOVA) and cluster analysis (CA) to obtain approximately normally distributed values. Cover variables used in logistic regression analyses were not transformed.

At the stand scale I used Pearson correlations to examine relationships between the average density of chestnut-backed chickadee breeding pairs at each site and the

density of (1) all trees, (2) dead trees, (3) diseased/attacked trees, and (4) trees with conks, blind conks, boring insects, broken tops, frost cracks, and brown needles. I first examined relationships between breeding density and stand characteristics for each year (2001, 2002, 2003) before pooling data across years to obtain the average density of breeding pairs at each site.

I used *K*-means cluster analysis (CA) to categorize random plot data collected at each of my 8 sites (uncut = 37 plots, partial cut-mature = 32 plots, partial cut-old = 20 plots) into groups based on 6 structural characteristics (tree cover, pole-sapling density, density of all trees, density of dead trees, density of diseased/attacked trees, and average DBH) instead of using the predetermined treatment classification. I used random plot data collected within each site over the 3 years of sampling (2000-2002) to cluster sites. I considered these data to be 1 time measurement. I assumed that small numbers of trees were lost each year due to mortality of live trees and loss of standing dead trees (wind events). I examined cluster membership and distance from cluster center for each random plot (case) to identify and interpret clusters. The 3 treatment-age groups defined by the cluster analysis, uncut (UC), partial cut-mature (PCM), and partial cut-old (PCO), were used to examine resource selection at the nest patch and nest tree scales. Using 3 treatment-age groups for these analyses allowed me to limit model development and maximize sample sizes relative to the number of predictor variables examined.

At the nest patch scale, I used a one-way analysis of variance (ANOVA) with nest name as a blocking effect to compare nest plots to close plots in each of the 3 treatment-age groups for all stem densities and average DBH. I used the non-parametric Friedman's test for all disease, insect, and damage variables (conks, blind conks, boring insects, broken tops, brown needles, frost cracks) that did not meet assumptions of

homogeneity of variances or normality. I compared 10 variables between nest plots and close plots: density of all trees, the density of dead trees, the density of diseased trees, the average DBH, and the density of trees with conks, blind conks, boring insects, broken tops, brown needles, and frost cracks. In similar analyses, I compared each of these 10 variables between nest plots and random plots within each treatment-age group. I used an alpha level of 0.05 for all univariate tests and treated these variables independently. To determine which variables were important for nest patch selection, I used forward stepwise logistic regression to compare habitat between nest plots and close plots using 12 plot level variables (9 structure and health agent variables given previously plus tree cover, shrub cover, and habitat type) in each treatment-age group. I first evaluated all nest patch variables for multicollinearity (correlated variables) by examining tolerance, conditioning index, and variance proportions; a conditioning index > 0.30 and 2 variance proportions for an individual variable > 0.50 were the criteria for multicollinearity. I removed the variable disease from my analysis because of correlations with specific health agents. I used a significance level of 0.15 to include and 0.10 to drop variables in all forward stepwise regression analyses. The logistic regression equation represented a resource selection function for nest site selection in relation to availability at the nest patch scale. Only 1 nest plot overlapped with a close plot (< 5 m). In all other cases, the distance between plot centers exceeded 8 m.

At the nest tree scale, I calculated a selection ratio for a variety of nest tree variables including tree species, tree status (dead or diseased), and the presence of specific health agents to determine which variables were important for nest tree selection. Selection ratios are defined as the proportion of used resource units in relation to the proportion of available resource units. For each resource unit the ratio is proportional to

the probability of that unit being utilized, given that the selecting organism has unrestricted access to the entire distribution of available units (Manly et al. 2002). I used tree species and tree characteristics as my resource categories. Nest trees were used resource units and non-nest trees within nest plots were available resource units. The selection ratio for category i was $\hat{w}_i = o_i/\pi_i$, where o_i is the ratio of nest trees (used) in category i to the total number of nest trees, and π_i is the ratio of non-nest trees (available) in category i to the total number of trees. Selection ratios greater than 1.0 indicate preference for a resource, while ratios less than 1.0 indicate avoidance (Manly et al. 1993). I calculated Manly's standardized selection ratio as $B_i = \hat{w}_i / (\sum \hat{w})$, which is the estimated probability that a category of resource units would be the next one selected if all types of resource units were equally available (Manly et al. 2002). Large values of B indicate a high probability that the resource will be selected, while small values indicate a low probability of selection. I illustrated the relative strength of selection among tree species using the inverse number of resources (i.e., $1/8 = 0.125$).

To determine which variables were important for nest tree selection, I used forward stepwise logistic regression to compare (1) nest trees to non-nest trees within nest plots, and (2) nest trees to trees within close plots using 10 tree level variables within the 3 treatment-age groups: tree species, wood condition (7 categories), DBH, whether the tree was dead, whether the tree contained conks, blind conks, boring insects, a broken top, brown needles, and frost cracks. Categorical variables were tree species, wood condition, and those related to disease, insects, and damage; the continuous variable was DBH. These logistic regression equations represented resource selection functions for nest tree selection in relation to availability within nest plots and close plots.

I used 2 criteria to assess all resource selection functions: (1) the goodness of fit or likelihood-ratio test (χ^2) = $2[(\log\text{-likelihood for full model}) - (\log\text{-likelihood for constant-only model})]$, and (2) the statistical significance of each coefficient (Wald test).

RESULTS

Forest Habitat Attributes in Uncut and Partial Cut Sites

The average stem density of all trees, dead trees, and diseased trees sampled in random plots was highest in uncut sites (Table 3.1). Although partial cutting reduced total stem density by approximately 50% (uncut: $x = 31.6$, partial cut: $x = 15.9$), the proportion of dead and diseased stems remained comparable to uncut sites (range in uncut: 60.2-87.0%; range in partial cut: 58.2-90.9%).

The occurrence of specific health agents differed among tree species (live and dead) found in Interior Cedar-Hemlock (ICH) stands (Appendix II). Stem rot diseases were not closely associated with any tree species, although the occurrence of these diseases appeared to increase in older sites. Breakage of tree tops occurred among all tree species but reached high levels (>60%) in paper birch trees. Boring insects which included spruce beetle, western balsam bark beetle, and other woody tissue feeders like weevils, were most abundant in hybrid spruce, subalpine and amabilis fir, and western hemlock. In general, among all trees surveyed in the random plots, boring insects occurred more frequently (46.8%) than all other health agents. Western hemlock, the dominant species in all sites had a low occurrence of stem rot diseases and broken tops, but exhibited the highest occurrence of boring insects.

Habitat Use at the Stand Scale

I examined the relationship between the density of breeding pairs of chestnut-backed chickadees in each of the 8 study sites and (1) the density of all trees, and (2) the

density of trees with various health agents. The average territory size of chestnut-backed chickadees within my sites was 4.5 ha ($n = 87$). The average density of chickadee breeding pairs calculated from complete and partial territories did not differ among treatment-age groups ($F_{2,5} = 2.40$, $P = 0.19$); uncut sites: $x = 0.20 \pm 0.02$ SE breeding pairs/ha (range = 0.13-0.23); partial cut-mature sites: $x = 0.15 \pm 0.02$ SE breeding pairs/ha (range = 0.12-0.18); partial cut-old sites: $x = 0.24 \pm 0.02$ SE breeding pairs/ha (range = 0.22-0.26). I found no significant correlations between the average density of breeding chickadees and the density of trees ($r = -0.42$, $P = 0.30$, $n = 8$), dead trees ($r = -0.51$, $P = 0.20$, $n = 8$), or diseased trees ($r = -0.03$, $P = 0.94$, $n = 8$). The density of chickadee pairs was not correlated with the density of trees with conks ($r = 0.28$, $P = 0.50$, $n = 8$), blind conks ($r = 0.24$, $P = 0.57$, $n = 8$), or boring insects ($r = -0.10$, $P = 0.82$, $n = 8$). Chickadee breeding pair density was not correlated with the density of trees with physical defects including broken top trees ($r = -0.44$, $P = 0.28$, $n = 8$), frost cracks ($r = -0.07$, $P = 0.86$, $n = 8$), or brown needles ($r = -0.19$, $P = 0.66$, $n = 8$).

Habitat Selection at the Nest Patch Scale

In uncut sites, univariate analyses (Table 3.2) indicated that chestnut-backed chickadee nest plots had higher densities of broken top trees than close plots ($\chi^2 = 7.14$, $df = 1$, $P = 0.008$). The density of dead trees was higher in nest plots than in random plots ($F_{1,56} = 4.03$, $P = 0.05$). The multivariate logistic model of nest patch selection also indicated that higher densities of broken top trees predicted nest plot use ($\chi^2 = 7.95$, $df = 1$, $P = 0.02$; Wald statistic = 2.21, $df = 1$, $P = 0.03$). The odds of using a nest plot was 1.6 times as likely with each 1 unit increase in broken top trees (odds increased by 63%; odds ratio = 1.63, CI: 1.06 to 2.51).

In partial cut-mature sites, I found no difference between nest plots and close plots for any of the variables I examined (Table 3.2). Nest plots had higher densities of diseased trees ($F_{1,59} = 7.81, P = 0.007$) and of trees infected with blind conks ($\chi^2 = 15.70, df = 1, P < 0.001$) and brown needles ($\chi^2 = 4.26, df = 1, P = 0.039$) than random plots. No habitat variables emerged as reliable predictors of nest plot use in the multivariate logistic regression analysis adding further support to my univariate analyses comparing nest and close plots.

In partial cut-old sites, univariate analyses (Table 3.2) indicated that nest plots had higher densities of trees ($F_{1,36} = 5.29, P = 0.03$), dead trees ($F_{1,36} = 5.53, P = 0.03$), and broken top trees ($\chi^2 = 10.29, df = 1, P = 0.001$) than close plots. Nest plots had higher densities of dead trees ($F_{1,37} = 9.34, P = 0.004$) than random plots. The multivariate logistic model of nest patch selection indicated that higher densities of broken top trees predicted nest plot use ($\chi^2 = 15.10, df = 1, P = 0.001$; Wald statistic = 2.65, $df = 1, P = 0.008$). The odds of using a nest plot was 2.6 times as likely with each 1 unit increase in broken top trees (odds ratio = 2.55, CI: 1.27 to 5.11).

Habitat Selection at the Tree Scale

Relative to their availability in nest plots, chestnut-backed chickadees in uncut sites preferred to nest in paper birch with about 29 times the probability of nesting in western hemlock ($B = 0.560/0.019$), and in trembling aspen with about 21 times the probability of nesting in western hemlock ($B = 0.394/0.019$; Figure 3.1). Within partial cut-mature sites, chestnut-backed chickadees preferred to nest in black cottonwood, paper birch, and trembling aspen relative to their availability in nest plots (Figure 3.2). In

partial cut-old sites, western hemlock and amabilis fir, the 2 most abundant species in these stands, were selected with approximately equal probability (Figure 3.3).

In uncut and partial cut-mature sites, selection ratio values indicate that chestnut-backed chickadees selected nest trees with conks and broken tops relative to their availability in nest plots. In uncut sites, nest trees with conks and broken tops were selected with about 4 to 5 times the probability of trees containing brown needles, while in partial cut-mature sites, nest trees with conks and broken tops were 3 times as likely to be selected as diseased trees. In partial cut-old sites, chickadees selected dead, broken top nest trees with approximately 30 times the probability of diseased trees (Table 3.3). Since nest plots and close plots had similar values of π (ratio of non-nest trees to total trees) for the tree characteristics examined (see Table 3.3), I will only present multivariate resource selection functions that predict nest tree use from available trees within the nest plot. In uncut sites, multivariate logistic regression analysis revealed that nest trees could be distinguished from other trees within a nest plot by the presence of boring insects, broken tops, and frost cracks ($\chi^2 = 92.76$, $df = 3$, $P < 0.001$; Wald statistic $P < 0.01$ for all estimated coefficients). In partial cut-mature sites, the presence of boring insects and broken tops predicted the use of nest trees within nest plots ($\chi^2 = 129.98$, $df = 2$, $P < 0.001$; Wald statistic $P < 0.01$ for all estimated coefficients). In partial cut-old sites, nest trees could be distinguished from other trees within the nest plot by the presence of large diameter trees and boring insects ($\chi^2 = 72.14$, $df = 2$, $P < 0.001$; Wald statistic $P < 0.002$ for all estimated coefficients).

Nest tree and nest placement characteristics of chestnut-backed chickadee nests in uncut, partial cut-mature, and partial cut-old sites are presented in Table 3.4. The average

nest height and tree height of chickadee nest trees was greatest in partial cut-mature sites, while nest tree diameter was greatest in partial cut-old sites. Chickadees used a variety of tree conditions across all sites, although live, predominantly healthy trees were selected most often in uncut and partial cut-mature sites (tree condition codes 1 and 2), while dead, broken top trees were selected in partial cut-old types (code 6). Average nest tree cover was highest in uncut sites (91%), although nest trees in all sites had nest cover >82%. Wood condition code 3 (wood essentially hard, limited decay) was the most frequent code in uncut and partial cut-mature sites, while code 4 (wood mostly hard, decay spreading with soft wood present) was most common in partial cut-old sites. The highest proportion of nest cavities in all sites occurred on the bole of the tree. Although natural cavity nests were the most common type of cavity used in all sites (uncut – 67%, partial cut-mature – 48%, partial cut-old – 53%), higher proportions of secondary cavity nests were used in partial cut-mature and partial cut-old (32-34%) sites compared to uncut sites (19%).

DISCUSSION

My results suggest that stand scale characteristics did not appear to influence the breeding density of chestnut-backed chickadees. Chickadees selected similar resources at the nest patch and nest tree scales across the treatments, but also exhibited flexibility in resource selection at the tree scale by using different tree species and tree conditions in each site. The type of nest tree selected by chestnut-backed chickadees appeared to shift with the species, condition, and size of available trees.

Stand Scale Habitat Use

Average densities of chestnut-backed chickadees ranged from 0.15 to 0.24 breeding pairs/ha across my study sites, comparable to 0.1 to 0.5 pairs/ha reported for

chestnut-backed and mountain chickadees (*Poecile gambeli*) in conifer forests (Erskine 1977). In my study area, uncut and partial cut-old sites had slightly higher densities of chickadee pairs than partial cut-mature sites, although I found no correlation between breeding pair density and structural characteristics of stands. Small number of sites examined likely resulted in low power to observe relationships between density and stand characteristics. Examining relationships between multiple structural variables and breeding density at a larger number of sites across a wider range of habitat conditions (harvest levels > 60%) may be needed to reveal patterns. Investigating the spatial arrangement and amount of broad habitat types (uncut forest, thinned forest, natural or harvested gap openings, riparian or wetland areas) within breeding territories may also reveal relationships between breeding density or territory size and stand characteristics.

Similar breeding densities across all stand types suggests that chestnut-backed chickadees can tolerate low to medium intensity harvesting. Chestnut-backed chickadees are thought to be edge sensitive (i.e., avoid edges) and negatively affected by first pass forest harvesting (George and Brand 2002, Hejl et al. 2002). Classifying species as edge sensitive is complicated, requiring researchers to test for edge avoidance using nest and territory locations (Villard 1998). Variation in patterns of edge avoidance for many species may depend on both landscape type and edge characteristics; edges in forest and agricultural landscapes may differ in contrast and vegetation structure (Imbeau et al. 2003). Within my study area, chickadees used a mosaic of habitat types found within partial cut stands: uncut and thinned forest, forest gaps, and edge habitat created at the gap-forest interface and at natural forest openings (streams, wetlands). Since edge habitats were interspersed throughout partial cut stands in my study area, habitat use by chickadees was likely not negatively influenced by edge.

Hejl et al. (2002) suggested that species adapted to moist forest types that historically form the most homogeneous landscapes due to low fire return intervals, should be negatively impacted by forest harvesting due to increased landscape heterogeneity. Harvest type and intensity should be considered when assessing impacts on forest birds at the territory, stand, or landscape scales. In my system, chestnut-backed chickadees appeared to display both (1) resistance to small-scale habitat changes, and (2) tolerance of habitat change up to 60% tree volume removal. Birds inhabiting forest types dominated by small-scale disturbances may be resistant to openings in the canopy created by harvesting because these simulate the natural disturbance events (wind, insects, disease) operating within these stands (Steventon et al. 1998, Chambers et al. 1999, Robinson and Robinson 1999, Leupin et al. 2004). In addition, partial cutting can maintain populations of weak cavity excavators by retaining the structural features associated with nesting habitat (broken tops, branch holes, wound sites) in sufficient quantity and quality. In the ICH zone in northwest British Columbia, the breeding densities of chestnut-backed chickadees and red-breasted nuthatches within treatment units at the Date Creek experimental site (uncut, clearcut, 30% and 60% partial cuts) did not differ among treatments 1 to 2 years and 9 years after harvesting (J. D. Steventon, unpublished data).

Nest Patch Scale Habitat Selection

Chickadees in uncut and partial cut-old stands selected nest plots with high densities of broken top trees relative to close plots. Selection for broken top trees was strongest in partial cut-old stands where total tree density was lower. The diverse tree species composition in partial cut-mature stands may have increased the availability and

variety of suitable nest patches for chickadees so that patches of trees with broken tops were not strongly selected.

Chestnut-backed chickadees may have selected nest patches containing higher densities of broken top trees because these trees may provide locations for chestnut-backed chickadees to successfully excavate a nest cavity. If nest cavities are located within patches of broken top trees, predators may find it difficult to locate the actual nest tree. Increasing the number of potential nest sites that must be searched by a predator may reduce the risk of nest predation (Martin 1993). Red squirrels (*Tamiasciurus hudsonicus*), the main predator of chickadees in my study area (Steventon et al. 1999; Chapter 2), use avian parental activity as a cue to locate nests (Martin and Li 1992; C. L. Mahon, personal observation). I frequently observed squirrels investigating trees and cavities near active nest sites, suggesting that squirrels used directed search techniques to locate nests. Selecting patches containing many potential nest sites may also facilitate rapid renesting in the event of nest loss from predation. In early spring, chickadees often excavated several nest sites before selecting a cavity in which to lay eggs (Smith 1993, Ficken et al. 1996, this study). Increased nesting area familiarity may be advantageous if high rates of nest predation result in renesting attempts. Within my study area, chestnut-backed chickadee nest failure reached 82% in 2001, with predators accounting for 64% of nest losses (Chapter 2). I observed renesting by chickadees in my study area in 2001, 2002, and 2003 and 2 second nesting attempts after successful first nests in 2003 (C. L. Mahon, personal observation).

Nest Tree Scale Habitat Selection

Chickadees in my study system exhibited flexibility in resource selection by selecting different tree species in different sites. Chestnut-backed chickadees nested in

deciduous trees in mature stands and in western hemlock and amabilis fir in old stands. Mature stands in the ICHmc subzone are dominated by western hemlock, but also contain a diverse mix of other conifer and deciduous species, but in the old-growth stage, only shade tolerant species like western hemlock, western redcedar, and amabilis or subalpine fir remain. Trembling aspen and paper birch may have been selected as nest trees because aggressive and rapid decay by heart rots like aspen trunk rot (*Phellinus tremulae*), hardwood trunk rot (*P. igniarius*), and white spongy trunk rot (*Fomes fomentarius*) can result in soft heartwood in living trees and soft heartwood and sapwood in dead trees (Harestad and Keisker 1989). In older stands, a higher proportion of conifers are in a sufficient stage of decay for chickadees to excavate a nest cavity. Thus chickadees can use conifers as nest trees as the stand ages. Despite using different tree species, chickadees selected trees with similar attributes (e.g., boring insects). The presence of boring insects may have indicated that the tree was in a weakened state or in a progressive state of decay.

Chickadees showed further flexibility in resource selection at the nest tree scale by selecting trees of different condition or size in the different sites. Although chickadees primarily selected nest trees with boring insects and broken tops in uncut and partial cut-mature sites, and large trees with boring insects in partial cut-old sites, the condition of these trees varied widely. In uncut and partial cut-mature sites, chickadees primarily used nest trees categorized as condition 1 (live and healthy) or 2 (live but unhealthy; some foliage and twigs lost; possible broken top). In partial cut-old sites, chickadees used nest trees categorized as condition 6 (dead; no branches; broken top). In addition, chickadees used larger trees in partial cut-old sites relative to uncut or partial cut-mature sites. My results indicate that the condition and size of nest trees selected by

chestnut-backed chickadees shifted with the condition and size of available trees.

Selection of nest trees across sites may vary due to differences in tree species characteristics (growth, lifespan, or disease susceptibility; Zwicker and Walters 1999) or site quality (soil, climate, competition). In the southeastern United States, the red-cockaded woodpecker (*Picoides borealis*) was considered to be limited by the availability of large, old pines. Selection studies in several locations revealed that woodpeckers selected the oldest available trees, but the age of selected nest trees shifted with the age of available pines (Rudolph and Conner 1991, Zwicker and Walters 1999, Walters et al. 2002).

My findings suggest that chestnut-backed chickadees can establish territories and nest in partial cut sites containing a variety of habitat types. Chickadees selected similar resources at the nest patch and nest tree scales in uncut and partial cut sites providing further evidence that specific attributes needed by this species for nesting (trees with broken tops and boring insects) were retained in partial cut sites. Although I have assessed patterns of habitat selection at the nest patch and nest tree scales separately, recent studies demonstrate approaches for quantifying and modeling cross-scale correlations (correlations among habitat variables across scales; Battin and Lawler 2006). My results also emphasize the importance of flexibility in resource selection patterns. Although small body and bill size limits weak cavity excavators like chickadees and nuthatches to nest trees with soft, decayed wood (Harestad and Keisker 1989, Albano 1992, Steeger and Hitchcock 1998, Martin et al. 2004), these species can utilize a variety of tree conditions and sizes, nest site locations, and cavity types. I suggest that within ICH forest types, weak cavity excavators may be resistant to the impacts of low to medium intensity harvesting because: (1) small scale disturbances (wind, insects,

disease) create structural diversity within stands, (2) partial cutting appears to maintain structural diversity within stands, and (3) these species can exhibit flexibility in their use of resources particularly with respect to nest trees and nest sites. In addition, the high diversity and occurrence of forest health agents (disease, insects, physical defects) within these forests may increase the availability of suitable nest sites for cavity nesters.

Resource type and availability may change in time and space depending on the type and scale of disturbance agent operating within the forest. Forest species that can shift their use of resources may be better able to adapt to habitat change resulting from forest harvesting.

Table 3.1. Stand scale characteristics of uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2002. Density is presented as stems/0.031 ha plots.

| | All stems | | Dead stems | | Diseased stems | | Dead or diseased ^c |
|---------------------------------|-----------|-----|------------|-----|----------------|-----|-------------------------------|
| Study site | <i>x</i> | SE | <i>x</i> | SE | <i>x</i> | SE | % |
| Uncut ^a | | | | | | | |
| C1 | 42.5 | 3.7 | 7.0 | 0.9 | 18.6 | 2.1 | 60.2 |
| HL7 | 29.2 | 3.1 | 4.2 | 0.7 | 18.0 | 1.8 | 76.0 |
| D3 ^b | 23.0 | 2.7 | 4.4 | 0.6 | 15.6 | 1.5 | 87.0 |
| Partial cut-mature ^a | | | | | | | |
| C3 | 17.5 | 2.1 | 5.0 | 0.6 | 10.9 | 2.1 | 90.9 |
| HL5 | 18.3 | 2.5 | 3.2 | 0.6 | 8.8 | 1.2 | 65.6 |
| C2 | 18.9 | 2.1 | 2.8 | 0.5 | 8.2 | 1.1 | 58.2 |
| Partial cut-old ^a | | | | | | | |
| D5 ^b | 15.0 | 2.7 | 2.2 | 0.4 | 10.1 | 2.5 | 82.0 |
| D4 ^b | 9.8 | 1.3 | 1.0 | 0.0 | 7.1 | 1.4 | 82.7 |

^aNumber of random plots in uncut ($n = 37$), partial cut-mature ($n = 32$), and partial cut-old sites ($n = 20$). Harvest level was approximate % volume removal: uncut = 0; partial cut-mature = C3 (30), HL5 (40), C2 (60), partial cut-old = D5 (30), D4 (60).

^bStand age--old growth (353-373 years). For all other sites, stand age--mature (145 years).

^cProportion dead or diseased.

Table 3.2. Patch scale tree characteristics and forest health agents comparing nest plots with: (1) close plots, and (2) random plots in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2003. Density is presented as stems/0.031 ha plots.

| | Nest plots | | Close plots | | P^a | Random plots | | |
|------------------------|------------|-----|-------------|-----|--------|--------------|-----|--------|
| | x | SE | x | SE | | x | SE | P^a |
| Uncut | $n = 21$ | | $n = 21$ | | | $n = 37$ | | |
| All stems | 32.1 | 3.3 | 32.8 | 2.9 | 0.742 | 31.5 | 2.2 | 0.281 |
| Dead stems | 6.0 | 0.6 | 5.4 | 0.4 | 0.251 | 5.2 | 0.5 | 0.050* |
| Diseased stems | 18.3 | 2.0 | 21.0 | 2.1 | 0.134 | 17.4 | 1.0 | 0.542 |
| Av. DBH (cm) | 28.7 | 1.5 | 27.8 | 1.2 | 0.411 | 28.5 | 1.1 | 0.832 |
| Conks | 3.4 | 0.5 | 4.2 | 0.6 | 0.593 | 3.4 | 0.4 | 1.000 |
| Blind conks | 7.5 | 1.0 | 6.5 | 0.9 | 0.157 | 7.2 | 0.9 | 0.251 |
| Boring insects | 15.1 | 2.1 | 17.9 | 2.3 | 0.251 | 14.8 | 1.1 | 0.827 |
| Broken tops | 3.5 | 0.5 | 2.1 | 0.4 | 0.008* | 2.7 | 0.3 | 0.157 |
| Brown needles | 3.8 | 0.9 | 4.4 | 1.0 | 1.000 | 7.2 | 0.8 | 0.251 |
| Frost cracks | 8.0 | 0.9 | 7.0 | 0.9 | 0.637 | 3.7 | 0.6 | 0.491 |
| Partial cut- mature | $n = 29$ | | $n = 29$ | | | $n = 32$ | | |
| All stems | 21.5 | 1.5 | 21.0 | 1.4 | 0.752 | 17.8 | 1.4 | 0.081 |
| Dead stems | 3.5 | 0.6 | 3.9 | 0.5 | 0.326 | 2.8 | 0.4 | 0.314 |
| Diseased stems | 13.1 | 1.2 | 12.6 | 1.1 | 0.635 | 8.8 | 0.8 | 0.007* |
| Av. DBH (cm) | 29.0 | 1.1 | 27.1 | 0.9 | 0.060 | 27.7 | 1.1 | 0.380 |

| | | | | | | | | |
|-----------------|---------------|-----|---------------|-----|--------|---------------|-----|--------|
| Conks | 2.2 | 0.5 | 1.4 | 0.3 | 0.414 | 1.4 | 0.2 | 0.827 |
| Blind conks | 5.1 | 0.6 | 3.8 | 0.6 | 0.117 | 3.3 | 0.4 | 0.001* |
| Boring insects | 9.4 | 1.1 | 10.5 | 1.2 | 0.317 | 8.0 | 0.8 | 0.683 |
| Broken tops | 2.4 | 0.4 | 2.3 | 0.3 | 1.000 | 2.1 | 0.3 | 0.835 |
| Brown needles | 1.4 | 0.5 | 1.1 | 0.3 | 0.134 | 3.7 | 0.5 | 0.039* |
| Frost cracks | 4.4 | 0.6 | 4.4 | 0.6 | 0.841 | 1.6 | 0.3 | 0.414 |
| Partial cut-old | <i>n</i> = 19 | | <i>n</i> = 19 | | | <i>n</i> = 20 | | |
| All stems | 15.6 | 1.9 | 11.2 | 1.2 | 0.033* | 11.4 | 1.5 | 0.079 |
| Dead stems | 3.5 | 0.8 | 1.7 | 0.4 | 0.030* | 0.8 | 0.2 | 0.004* |
| Diseased stems | 11.9 | 1.8 | 8.8 | 1.2 | 0.085 | 8.0 | 1.3 | 0.076 |
| Av. DBH (cm) | 38.6 | 2.3 | 37.7 | 1.7 | 0.692 | 38.3 | 2.8 | 0.895 |
| Conks | 4.5 | 0.7 | 3.0 | 0.6 | 0.317 | 2.6 | 0.5 | 0.071 |
| Blind conks | 3.8 | 0.7 | 3.8 | 0.7 | 0.225 | 2.8 | 0.5 | 0.796 |
| Boring insects | 8.9 | 1.5 | 6.1 | 1.2 | 0.225 | 5.7 | 0.9 | 0.593 |
| Broken tops | 3.4 | 0.8 | 0.8 | 0.3 | 0.001* | 0.9 | 0.2 | 0.166 |
| Brown needles | 2.5 | 0.8 | 1.6 | 0.6 | 0.248 | 4.4 | 0.6 | 0.796 |
| Frost cracks | 6.3 | 1.0 | 4.4 | 0.8 | 0.491 | 1.7 | 0.5 | 0.617 |

^a*P* values for stem densities and average DBH from one-way analysis of variance with nests as blocking effect. *P* values for disease, insect, and damage variables (conks, blind conks, boring insects, broken tops, brown needles, frost cracks) from Friedman's test.

Table 3.3. Selection of tree scale characteristics from trees available within nest plots in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2003. Tree characteristics in close plots are shown for comparison.

| Characteristics | Nest plots | | | | Close plots |
|--------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------|
| | Nest trees | | All trees | | All trees |
| | <i>n</i> = 69 | | <i>n</i> = 653 | | <i>n</i> = 690 |
| | <i>o</i> ^a | <i>π</i> ^b | <i>w</i> ^c | <i>B</i> ^d | <i>π</i> |
| Uncut | | | | | |
| Dead | 0.571 | 0.176 | 3.244 | 0.134 | 0.164 |
| Diseased | 0.905 | 0.556 | 1.628 | 0.067 | 0.626 |
| Conk | 0.476 | 0.096 | 4.958 | 0.205 | 0.128 |
| Blind conk | 0.476 | 0.228 | 2.088 | 0.086 | 0.197 |
| Boring insect | 0.762 | 0.462 | 1.649 | 0.068 | 0.545 |
| Broken top | 0.619 | 0.093 | 6.656 | 0.275 | 0.064 |
| Brown needle | 0.143 | 0.119 | 1.202 | 0.050 | 0.135 |
| Frost crack | 0.667 | 0.242 | 2.756 | 0.114 | 0.213 |
| Partial cut-mature | | | | | |
| Dead | 0.552 | 0.148 | 3.730 | 0.179 | 0.187 |
| Diseased | 0.966 | 0.597 | 1.618 | 0.078 | 0.594 |
| Conk | 0.448 | 0.091 | 4.923 | 0.236 | 0.069 |
| Blind conk | 0.448 | 0.233 | 1.923 | 0.092 | 0.181 |
| Boring insect | 0.828 | 0.426 | 1.944 | 0.093 | 0.498 |
| Broken top | 0.483 | 0.096 | 5.031 | 0.242 | 0.110 |

| | | | | | |
|-----------------|-------|-------|--------------|--------------|-------|
| Brown needle | 0.000 | 0.067 | 0.000 | 0.000 | 0.051 |
| Frost crack | 0.345 | 0.208 | 1.659 | 0.080 | 0.210 |
| Partial cut-old | | | | | |
| Dead | 0.684 | 0.194 | 3.526 | 0.269 | 0.151 |
| Diseased | 1.000 | 0.773 | 0.1294 | 0.010 | 0.792 |
| Conk | 0.421 | 0.281 | 1.498 | 0.114 | 0.269 |
| Blind conk | 0.526 | 0.248 | 2.121 | 0.162 | 0.344 |
| Boring insect | 1.000 | 0.561 | 0.1782 | 0.014 | 0.547 |
| Broken top | 0.789 | 0.191 | 4.131 | 0.315 | 0.071 |
| Brown needle | 0.000 | 0.173 | 0.000 | 0.000 | 0.142 |
| Frost crack | 0.632 | 0.410 | 1.541 | 0.117 | 0.396 |

^a o was the ratio of nest trees (used) to the total number of nest trees.

^b π was the ratio of non-nest trees (available) to the total number of trees.

^c \hat{w} was the selection ratio ($\hat{w} = o/\pi$), the proportion of used resources versus the proportion of available resources. Selection ratios > 1.0 indicate preference for a resource, while selection ratios < 1.0 indicate avoidance.

^d B was Manly's standardized selection ratio [$B = \hat{w}/(\sum \hat{w})$], the probability that a resource was selected next if all types of resources were equally available. Large values of B (bold in table) indicate a high probability that the resource was selected, while small values indicate a low probability of selection (e.g., a resource with $B = 0.200$ was about 2 times as likely to be selected as a resource with $B = 0.100$).

Table 3.4. Average nest tree and nest placement characteristics of chestnut-backed chickadee nests in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2003.

| | Uncut | Partial cut- mature | Partial cut- old |
|---|---------------|------------------------|---------------------|
| Nest tree | <i>n</i> = 21 | <i>n</i> = 29 | <i>n</i> = 19 |
| Tree height (m) | 16.3 | 22.2 | 14.2 |
| Tree DBH (cm) | 31.9 | 40.2 | 43.8 |
| Tree condition (mode; range) ^a | 2; 1 – 7 | 1; 1 – 7 | 6; 1 - 7 |
| Wood condition (mode; range) ^b | 3; 2 – 7 | 3; 2 – 6 | 4; 2 - 5 |
| Nest placement | | | |
| Nest height (m) | 11.0 | 13.6 | 8.1 |
| Nest tree cover (%) | 91.2 | 81.8 | 85.9 |
| Number of cavities ^c | 1.3 | 1.7 | 2.2 |
| Nest position | | | |
| Bole | 16 | 29 | 15 |
| Top | 3 | 0 | 4 |
| Branch | 2 | 0 | 0 |
| Cavity type ^d | | | |
| Natural | 14 | 14 | 10 |
| Primary | 3 | 4 | 3 |
| Secondary | 4 | 10 | 6 |
| Unknown | 0 | 1 | 0 |

^aTree condition codes were (1) live tree; all foliage, twigs, branches present, (2) live tree; some foliage and twigs lost; all branches present; possible broken top, (3) dead tree; no foliage present and up to 50% of twigs lost; most branches present; possible broken top, (4) dead tree; no foliage or twigs present; up to 50% of branches lost; top usually broken, (5) dead tree; most branches lost but some branch stubs remain; top broken, (6) dead tree; no branches present but some sound and rotting branch stubs; top broken, (7) dead tree; some rotting branch stubs; stem broken.

^bWood condition codes were (1) no decay, (2) probably limited decay, (3) wood essentially hard; limited decay, (4) wood mostly hard but decay spreading; soft wood present, (5) balance of hard and soft wood; spongy sections, (6) more soft and spongy wood than hard wood, (7) no hard wood; all soft and spongy; powdery sections.

^cThe number of cavities in the nest tree.

^dNatural cavities were located in branch holes, cracks, wound sites, and broken tops. Primary cavities were excavated entirely by chestnut-backed chickadees. Secondary cavities were excavated by weak cavity excavators (nuthatches) or strong cavity excavators (woodpeckers) and renovated by chestnut-backed chickadees.

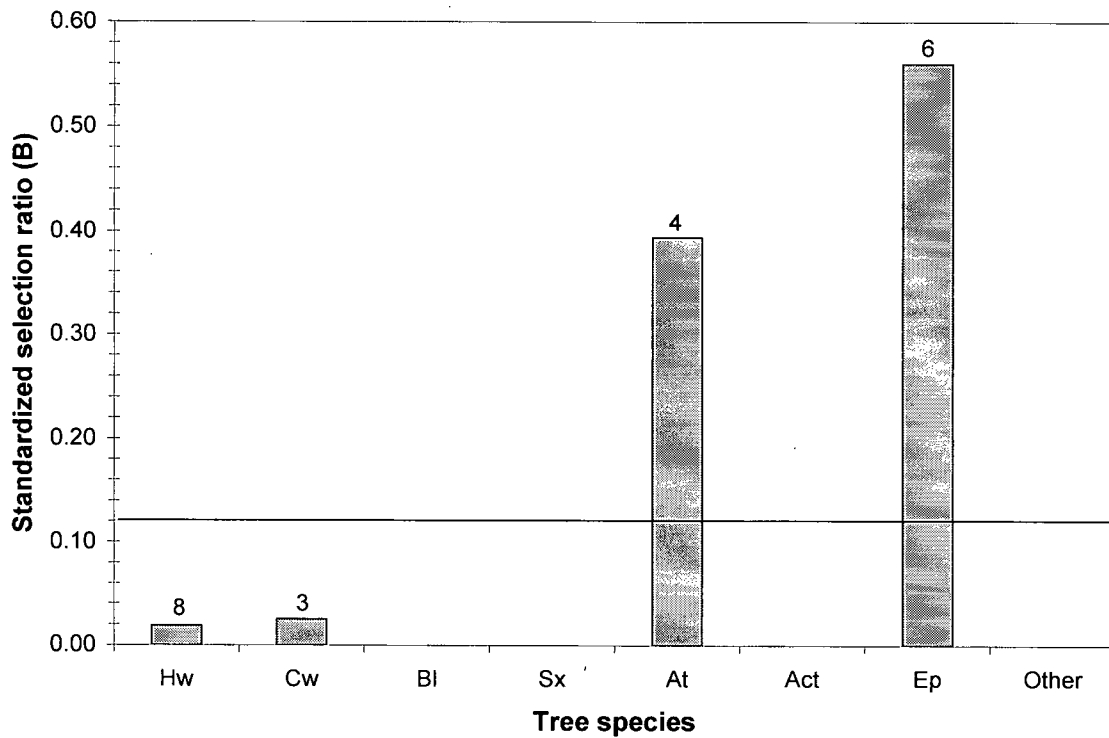


Figure 3.1. Selection of chestnut-backed chickadee nest tree species within nest plots in uncut sites at McCully Creek, British Columbia. Standardized selection ratio (B) was the probability that a resource (tree species) was selected next if all types of resources were equally available. Numbers above bars were sample sizes of nests. The solid line represents the level of selection if all tree species were selected at random. Tree species were: western hemlock (Hw), western redcedar (Cw), subalpine fir (Bl), hybrid spruce (Sx), trembling aspen (At), and black cottonwood (Act), paper birch (Ep).

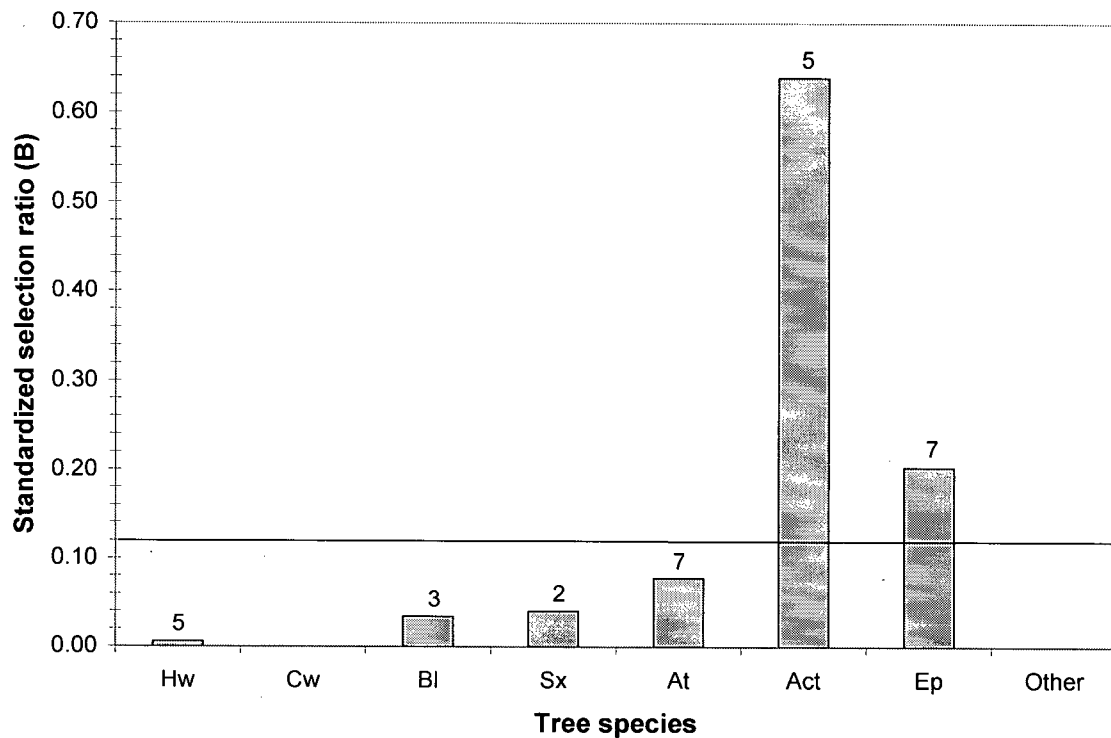


Figure 3.2. Selection of chestnut-backed chickadee nest tree species within nest plots in partial cut-mature sites at McCully Creek, British Columbia. Standardized selection ratio (B) was the probability that a resource (tree species) was selected next if all types of resources were equally available. Numbers above bars were sample sizes of nests. The solid line represents the level of selection if all tree species were selected at random. Tree species were: western hemlock (Hw), western redcedar (Cw), subalpine fir (Bl), hybrid spruce (Sx), trembling aspen (At), and black cottonwood (Act), paper birch (Ep).

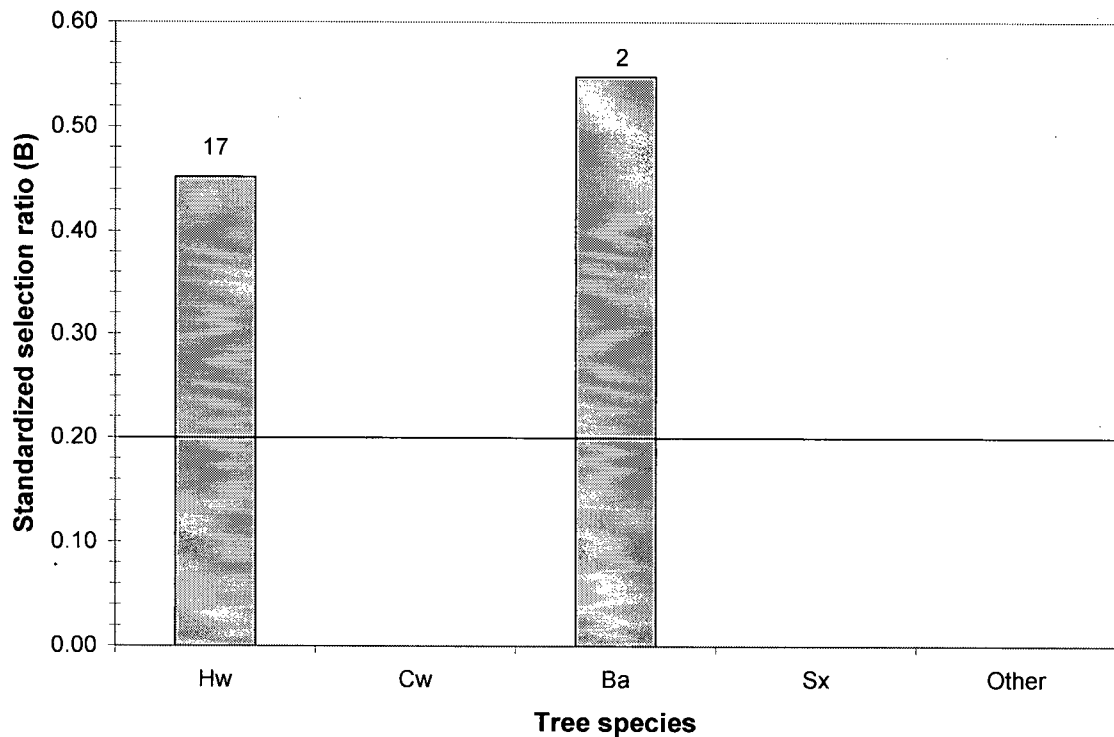


Figure 3.3. Selection of chestnut-backed chickadee nest tree species within nest plots in partial cut-old sites at McCully Creek, British Columbia. Standardized selection ratio (B) was the probability that a resource (tree species) was selected next if all types of resources were equally available. Numbers above bars were sample sizes of nests. The solid line represents the level of selection if all tree species were selected at random. Tree species were: western hemlock (Hw), western redcedar (Cw), amabilis fir (Ba), hybrid spruce (Sx).

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CHAPTER 4:
THE INFLUENCE OF FOOD AVAILABILITY, PREDATOR PRESSURE, AND
NESTING HABITAT ON CHESTNUT-BACKED CHICKADEE
REPRODUCTIVE OUTPUT

INTRODUCTION

The reproductive success of forest birds can be influenced by a variety of separate and interacting factors including food abundance (Sillet et al. 2000), predation pressure (King 1983, Schmidt and Ostfeld 2003), habitat characteristics near the nest (Li and Martin 1991, Martin 1993), and availability of suitable nest sites (Hooze et al. 1999). For conifer-associated cavity nesters, changes in habitat structure resulting from forest harvesting may limit the number of live trees available for foraging (Weikel and Hayes 1999), and the diseased, damaged, or dead trees available for nesting (Mannan and Meslow 1984, Dobkin et al. 1995, Martin et al. 2004). Suitable nest trees may be limited in managed forests where dead or dying trees are removed to meet safety requirements (Zarnowitz and Manuwal 1985, Hunter 1990, Steeger and Hitchcock 1998).

Annual changes in food abundance for insectivorous forest birds can occur due to regional climatic influences (Jones et al. 2003) or natural insect cycles that increase from endemic (low) to epidemic (high) levels (Machmer and Steeger 1994, Canadian Forest Service 2001). Defoliating caterpillar outbreaks can increase the abundance (Holmes et al. 1986, Holmes and Sherry 2001, Jones et al. 2003) and reproductive success (Sillet et al. 2000) of insectivorous forest songbirds. Cavity nesting species in North America can also exhibit increases in abundance in response to changes in their food supply (Crawford and Jennings 1989, Connor et al. 1999, Martin et al. 2006). In Europe, annual variation

in caterpillar abundance influenced nestling diet (Bańbura et al. 1994) and both success and weight of fledging blue tits (*Parus caeruleus*; Tremblay et al. 2003).

Recent evidence suggests that annual changes in predator density may influence nest predation rates of forest birds. In deciduous forests of eastern North America, generalist predators like mice may exhibit numerical responses to changes in acorn production resulting in high rates of nest predation on forest songbirds (McShea 2000, Schmidt et al. 2001, Schmidt 2003). In conifer forests, red squirrels (*Tamiasciurus hudsonicus*) are an important predator of songbirds (Sieving and Willson 1998, Tewksbury et al. 1998). Annual variation in cone crops is related to red squirrel population density (Smith 1968, Kemp and Keith 1970) and reproductive success (Rusch and Reeder 1978, Wheatley et al. 2002). Following a cone mast event (year t), squirrel numbers may be larger due to higher over-winter survival or possibly higher reproductive success or juvenile production (year $t + 1$). As cone supplies become depleted but squirrel densities remain high, squirrels may need to search for and consume alternate food items (e.g., bird eggs, and nestlings). Whether interactions between seed production, squirrel abundance, and songbird nest predation rates occur in North American conifer forests is unknown.

Chestnut-backed chickadees occupy breeding territories within mature and old-growth stands within humid coastal and interior forests that provide live trees for foraging, and diseased, damaged, or dead trees for nesting (Dahlsten et al. 2002). Harvesting procedures like partial cutting attempt to maintain structural characteristics of stands and conserve habitat for wildlife species associated with mature and old-growth forests (Steventon et al. 1998). Changes in habitat structure could reduce the availability of foraging habitat and nest sites within chickadee territories, resulting in lower

reproductive output. However, chestnut-backed chickadees breeding within uncut and partial cut sites established territories at similar densities and exhibited flexibility in nest site selection, using a variety of tree conditions and sizes, nest site locations, and cavity types (Chapter 3). Nesting habitat (nest patch, nest tree characteristics) selected by chickadees may influence reproductive success (i.e., fitness consequences of selection). Alternatively, chickadee reproductive output could be strongly influenced by breeding territory characteristics such as food availability and predator density. Although chickadees can respond rapidly to temporal changes in the abundance and spatial distribution of their prey (Robinson and Holmes 1982, Kleintjes and Dahlsten 1995), regional scale factors may limit the annual abundance of main prey items (arthropods). In addition, chestnut-backed chickadees may be affected by high annual variation in nest predation rates possibly resulting from changes in predator density. Chestnut-backed chickadees can suffer rates of nest predation similar to those of cup nesting species (Chapter 2).

In this study, my objective was to examine whether the relative influence of (1) annual differences in food abundance and predation pressure, or (2) habitat structure, had a larger effect on the annual reproductive output of chestnut-backed chickadees. Study sites were characterized as uncut sites, partial cut-mature sites, and partial cut-old sites representing a gradient of forest sites containing small and large treefall gaps surrounded by a matrix of uncut or thinned forest. Uncut sites contained infrequent small natural gaps, while partial cut-mature sites contained small gaps (e.g., 30% volume removal) or small to large harvested gaps (40% and 60% volume removal) surrounded by thinned forest. Partial cut-old sites contained both natural and harvested gaps within a thinned forest matrix, with gap sizes ranging from small to large depending on harvest intensity

and natural disturbances found within sites. Chestnut-backed chickadees, like other conifer-associated chickadee species, forage for defoliating insects in the canopy of live, mature conifer and deciduous trees (Dahlsten et al. 2002). I predicted that years indicating an increase or outbreak of canopy defoliating insects would result in higher annual reproductive output at all sites. Interactions between year and habitat might result in the highest reproductive output in sites with high tree density, large tree size, and high amounts of above-ground biomass (e.g., foliage, branch, stemwood). Generalist predators like rodents may exhibit numerical responses to changes in food availability resulting in year-to-year fluctuations in density (McShea 2000, Schmidt 2003, Martin and Joron 2003). I predicted that years with high densities of red squirrels would result in higher rates of nest predation and lower annual reproductive output of chestnut-backed chickadees at all sites. Interactions between year and habitat might result in the highest reproductive output in sites containing low suitability squirrel habitat (low density of cone-producing conifers). I predicted that lower tree density (as a result of thinning and gap openings) and fewer large, diseased, or damaged trees in partial cut-mature sites would limit the availability of foraging areas and potential nest sites resulting in lower reproductive output (daily nest survival, productivity) in these sites in all years. Uncut sites would have the highest reproductive output in all years.

STUDY AREA

My study area was within the McCully Creek watershed, approximately 35 km north of the town of Hazelton, British Columbia, Canada, in the Interior Cedar-Hemlock moist cold (ICHmc) biogeoclimatic ecological subzone (see Chapter 1).

I established 3 uncut and 5 partial cut sites (19-24 ha) ranging from low intensity harvest (30% of the stand volume as single trees and small patch cuts) to high intensity

harvest (60% of the stand volume with 30% in openings of 0.1 to 0.5 ha and 30% as single trees between openings; Coates et al. 1997). In partial cut sites, trees were removed across all species and diameter classes. Time since harvest for partial cut stands ranged from 3 to 8 years. All study sites were within mature and old forest stands (>145 years) and contained 50 m x 50 m grid systems.

METHODS

Foraging Patterns

To describe habitat use by foraging chickadees, I recorded information on site characteristics (habitat type, vegetation layer), vegetation (size), and behaviour (foraging height, substrate, activity, feeding frequency, time spent off the nest). I observed foraging chickadees to determine if inter-annual changes in prey abundance altered foraging habitat use and behaviour. I was unable to measure insect abundance directly due to tall canopy heights (30-40 m) and high tree species diversity within sites.

I observed foraging adults during the nestling stage from a sub-sample of active nests within each site during 2001 and 2002. I included foraging data collected during 3 within-day observation periods (1 = 6-9 am, 2 = 9-12 pm, and 3 = 12-3 pm) during days 7-12 of the nestling stage. I observed foraging adults for a minimum of 5 foraging bouts during each visit to a nest. A foraging bout was defined as 1 adult exiting the nest cavity and foraging in 1 or more trees before returning to the nest. I recorded foraging observations within a foraging bout and considered a change in foraging mode or activity, substrate, or location the start of a new observation. I recorded either single observations or up to 5 sequential observations (maximum) within a foraging bout. I assigned a value of 1 to each foraging bout and assigned weights according to the number of observations within a foraging bout (e.g., weighted values ranged from 1 to 0.20 if the maximum of 5

observations were obtained during a foraging bout). Because birds were often difficult to see due to foliage density and height, I recorded sequential foraging observations for some individuals to increase the amount of information collected. Using this method, I incorporated all data collected without biasing individuals that contributed multiple observations (Airola And Barrett 1985). Data collected during each foraging observation included: habitat type (forest, thinned forest, forest gap, forest edge, riparian, riparian edge), vegetation layer (tree, high shrub, low shrub), vegetation size (diameter at breast height), foraging height, substrate type (trunk, branch, twig, foliage, cone, terminal bud, fallen log, fallen branch, debris pile, lichen, moss, ground, air), and foraging activity (glean, hang, hawk/flycatch, hover-glean, lunge, probe, peck, flake). Edges were found at the junction of 2 plant communities (riparian edge – mature forest and riparian area) or 2 successional stages (forest edge – mature forest and early seral habitat found in gap openings or trails).

Predation Pressure

To assess predation pressure for chestnut-backed chickadees, I obtained an index of squirrel density within each site as part of a concurrent study of chestnut-backed chickadee nest survival. I conducted squirrel sign surveys during early July in 2001-2003 by surveying grid lines at 100 m intervals and obtained the average number of feeding sign detections/ha (mean of all transects) as an index of squirrel density and predation pressure at each site in each year (see Chapter 2).

Habitat Structure

I recorded vegetation and tree characteristics in 10 m radius circular plots centered at all active nest trees (nest plot) and random plots. The nest plot was used to describe the nest patch and the nest tree. To describe forest structure, each uncut and

partial cut site was divided into 4 quadrants from which a random plot was selected. Within all plots I used ocular estimation to assess percent cover of vegetation layers: tree; total shrub; herb; and moss, lichen, and seedling layers. I counted the number of live shrubs and saplings (< 12.5 cm DBH) for each species detected within the random plot. I recorded whether each tree > 12.5 cm was live or dead, measured tree diameter at breast height (DBH), and assessed tree health. I recorded the presence of physical defects and classified a tree as diseased/attacked if I detected stem rot, root disease, butt rot, trunk gall, mistletoe, other fungi, or boring insects. I followed the tree mensuration procedures in Field Manual for Describing Terrestrial Ecosystems (BC Ministry of Forests 1998). I used a clinometer to measure the height of nest trees and nest cavities, and I used a spherical densiometer to measure foliage density (cover) around the nest tree. I counted the total number of cavities in the nest tree. Random plots were sampled from 2000 to 2002 in order to establish a total of 8-12 random plots per site (approximately 1.6-2.5/ha). Nest plots were sampled at the end of the nesting cycle from 2001 to 2003.

Reproductive Output

I located nests by observing the breeding behaviour of adult birds which included: boundary disputes with neighbouring pairs, courtship vocalizations and displays, copulation events, nest excavation or renovation, and incubation or brooding behaviour. Nests were marked with flagging tape located > 10 m from the nest, and monitored every 2 to 3 days until the nest failed or young fledged. Evidence of nest predation included one of the following: an enlarged cavity entrance, nest material pulled out to the cavity entrance, and eggshell or nestling remains at the base of the nest tree. Predator species were identified by incisor marks or fresh claw marks around the cavity entrance and hair

located on the tree bole near the cavity (Chapter 2). I recorded nest fate as successful (at least 1 young fledged from the nest) or failed (no young fledged from the nest) and counted the minimum number of fledged young by observing young leave the nest cavity or observing adults feeding newly fledged young near the nest tree. I increased my nest monitoring effort close to predicted fledge dates in order to observe fledge events. Due to inaccessible nest locations and tall canopy heights (30-40 m), chickadee pairs were not colour-banded. I included nests located from 2001 to 2003 because indices of predator density were collected during these 3 years.

Statistical Analyses

I summarized foraging habitat use data for all chickadee pairs (total individuals = 56) observed within sites in 2001 ($n = 10$ pairs) and 2002 ($n = 18$ pairs). To assess use of site characteristics I calculated the proportion of each habitat type and vegetation layer used by foraging chickadees. To examine vegetation use, I calculated the proportion of foraging observations within vegetation size categories (15 cm size classes based on diameter at breast height). I examined foraging behaviour of chickadees by summarizing the proportion of foraging observations within height, substrate, and activity categories.

I used the number of feeding sign detections (age = recent)/ha within each site in 2001, 2002, and 2003 as an index of squirrel density and a measure of predation pressure. I used a one-way ANOVA to compare the indices of predator density among years. I used Pearson correlations to examine relationships between the index of predator density (feeding sign/ha) and (1) DMR, and (2) the minimum number of young fledged in 2001, 2002, and 2003.

I calculated average values for 3 vegetation cover (tree, high shrub, low shrub) and 5 vegetation structure variables (density of all trees, dead trees, diseased trees, tall

shrubs/saplings, average DBH) from all random plot data collected within each site over the 3 years of sampling to compare structural characteristics of sites. I considered this data to be 1 time measurement and assumed that small numbers of trees were lost each year due to mortality of live trees and loss of standing dead trees (wind events). I used forward stepwise logistic regression to predict nest outcome (successful vs. depredated) using habitat structure variables collected at the nest patch and nest tree. I included all successful nests and all failed nests that were known to be depredated during 2001-2003 ($n = 48$) in the nest patch and nest tree models. To limit the number of variables relative to sample sizes, I included all significant variables in univariate and multivariate analyses of nest patch and nest tree selection (Chapter 3). Nest patch variables entered into the nest patch model were density of all trees, dead trees, and trees with blind conks, broken tops, and brown needles. Nest tree variables entered into the nest tree model were DBH, whether the tree was dead, and whether it contained conks, boring insects, a broken top, or frost cracks. I used a significance level of 0.15 to include and 0.10 to drop variables in all forward stepwise regression analyses. I used these analyses to first determine if nest site attributes (nest patch, nest tree) selected by chickadees also predicted reproductive success. I could then compare the availability of these nest patch and nest tree attributes across sites.

For each nest, I estimated exposure days or nest age from the first day a nest was observed active to the day a nest failed or fledged. For nests with known fate (success or fail), the last exposure day was the midpoint between the last day the nest was checked and the previous visit. For nests with unknown fate, the last exposure day was the last day the nest was known to be active (last active date). These procedures generally result in the least bias (Manolis et al. 2000). At each site, I calculated daily mortality rate

(DMR), by dividing the number of failed nests by the total number of nest exposure days (Mayfield 1975), and predator daily mortality rate (PDMR) by dividing the number of nests destroyed by a predator by the number of nest exposure days. From the PDMR I calculated the proportion of nests depredated (when extrapolating the PDMR to a 33 day nesting cycle) as: $(1 - \text{PDMR})^d$, where d is the number of days in the nesting cycle (incubation and nestling period) of chestnut-backed chickadees (Schmidt and Ostfeld 2003). As a measure of productivity for each nest, I used the minimum number of young that successfully fledged from each nest (minimum number of young/nest/year). I used the non-parametric Kruskal-Wallis test to examine differences among years for DMR, PDMR, and productivity at each site because assumptions of normality and homogeneity of variances were not met for these variables. For calculations of daily nest mortality, I included all active nests detected in each site during 2001 to 2003 ($n = 60$).

RESULTS

Foraging Patterns

Chestnut-backed chickadees exhibited similar patterns of foraging habitat use and behaviour across sites, but changed their use of foraging sites by using different vegetation layers between years. Forest edge habitat was the most frequently used habitat type by foraging chickadees in both 2001 (range of use: 33.3-65.0%) and 2002 (range of use: 35.0-75.4%). Although in both 2001 and 2002, chestnut-backed chickadees foraged predominantly in the tree layer (2001 tree layer use: 99.7 ± 0.3 , range: 97.7-100.0%; 2002 tree layer use: 88.8 ± 0.5 , range: 66.1-97.5%), the number of vegetation layers used by foraging chickadees differed between years. In 2001, pairs in only 1 site ($n = 3$ pairs) used multiple vegetation layers when foraging, while in 2002, pairs in all sites ($n = 18$ pairs) used multiple vegetation layers (tree, high shrub, low shrub) when foraging.

The size of vegetation used for foraging by chickadees varied between years. In 2001, chestnut-backed chickadees foraged predominantly in mature trees (30.1-45.0 cm DBH size category; Figure 4.1A). By comparison, in 2002 chickadees in only 3 sites (D3, C3, HL5) used mature trees in proportions higher than other vegetation categories (Figure 4.1B). Pairs in all sites except C3 (partial cut-mature) showed greater use of vegetation in the 1.0-15.0 cm DBH or 15.1-30.0 cm DBH size categories (intermediate, suppressed, and regenerating conifers, deciduous saplings and shrubs).

Chickadees changed their foraging behaviour between years by foraging at lower heights (below the main canopy) and using different foraging activities or modes. Chestnut-backed chickadees foraged predominantly at heights of 10.1-20.0 m in both years, although chickadee pairs in all sites also foraged at lower heights (0-4.0 m) in 2002 (Figure 4.2A and B). Foliage was the dominant substrate used by foraging chestnut-backed chickadees in both years (2001 foliage range of use: 82.7-95.0%; 2002: 79.9-97.0%). Although gleaning (removing stationary prey from the substrate surface while perched) was the dominant foraging activity used in all sites in 2001 and 2002, chickadees increased their use of hanging to obtain prey in 2002 (2001 range of use: 10.0-32.8%; 2002: 25.3-59.8%; Figure 4.3A and B).

Predation Pressure

Detections of squirrel feeding sign were highly variable among the 8 sites in each year (2001 range: 5.0-69.4 feeding sign/ha; 2002 range: 10.0-35.4 feeding sign/ha; 2003 range: 15.6-48.9 feeding sign/ha). In all years, both the lowest and highest number of detections of feeding sign were located in uncut sites (Figure 4.4). My indices of predator density did not differ among years ($F_{2,21} = 1.51$, $P = 0.25$). Scatterplots and correlations between indices of predator density and DMR in each year revealed no

significant relationships (all $P > 0.05$). In 2003, a weak negative correlation between predator density and productivity indicated that as feeding sign/ha within a site increased, the minimum number of young fledged/nesting attempt decreased ($r = -0.66$, $P = 0.075$, $n = 8$).

Habitat Structure

Percent tree cover decreased with increasing harvest level, with the exception of D5, a low-intensity (30% tree volume removal) partial cut-old site. This site had large trees with high amounts of above-ground biomass (amount of foliage, branch, stemwood, stembark). High amounts of windthrow in the high-intensity, partial cut-old site (D4) resulted in lower cover estimates in this site relative to site D5 (Coates 1997). Average high shrub cover (2-10 m tall) increased with level of partial cutting in both partial cut-mature and partial cut-old sites, but was highest in the uncut-old site (Table 4.1). The amount of low shrub cover (< 2 m tall) in the uncut-old and partial cut sites was on average 4-6 times higher than uncut-mature sites.

Uncut sites contained the highest densities of all trees, dead trees, and diseased trees, while partial cut sites had tree densities that were reduced by approximately 50% (uncut: $x = 31.6$, partial cut: $x = 15.9$; Table 4.2). The average density of tall shrubs/saplings (< 12.5 cm dbh) was high in the uncut-old and partial cut sites (range: 182.7-201.6 stems/0.031 ha; Table 4.2). The largest trees were found in old sites (range: 34.6-42.9 cm DBH) compared to mature sites (range: 25.0-30.8 cm DBH).

The nest patch logistic model indicated that the density of broken top trees was a significant predictor of nest outcome ($\chi^2 = 4.42$, $df = 1$, $P = 0.036$; Wald test = 1.89, $df = 1$, $P = 0.059$). The odds of a successful nest was 0.79 times more likely with a 1 unit

increase in the number of broken top trees (odds decreased by 21%; odds ratio = 0.79, CI: 0.62 to 1.01). No variables were predictors of nest outcome in the nest tree logistic model at $P < 0.05$.

Reproductive Output

All measures of reproductive success showed high annual variation, but no consistent patterns across sites (Table 4.3). Although I observed high rates of daily mortality (DMR) in 2001 compared to 2002 and 2003, I found only modest variation in reproductive success among the 3 years ($\chi^2 = 5.40$, $df = 2$, $P = 0.07$, $n = 24$). The minimum number of young fledged (productivity) at each site differed among years ($\chi^2 = 7.90$, $df = 2$, $P = 0.02$, $n = 24$). Predator daily mortality rate (PDMR) also differed among years ($\chi^2 = 9.11$, $df = 2$, $P = 0.01$, $n = 24$) with the highest values in 2001 (Table 4.4).

DISCUSSION

Nesting habitat (nest tree and nest patch) did not have the largest influence on chestnut-backed chickadee reproductive output. Instead, characteristics associated with the larger breeding territory influenced the reproductive output and foraging patterns of chickadees. Predation pressure, which varied among years due to changes in predator habitat conditions, had the strongest influence on annual reproductive output of chickadees. Foraging habitat (and associated food availability) appeared to influence the foraging patterns of chickadees between years.

I observed high annual fluctuations in predator daily mortality rate in all of my sites. Squirrels were the primary nest predators in my study area and were responsible for the failure of 74% of depredated nests (Chapter 2). I suggest that annual variation in nest predation rates may be due to changes in resource availability for red squirrels.

Squirrels consume and cache the seeds of conifer cones which can vary widely in their availability from year to year due to cone mast and failure events (Koenig and Knops 2000). The annual abundance of cone crops is known to influence the population density (Kemp and Keith 1970) and reproductive success of red squirrels (Rusch and Reeder 1978, Wheatley et al. 2002). A mast failure event in the fall of 1999 and 2000 may have limited seed availability for red squirrels causing them to undergo a functional response and prey on chickadee nests during the 2001 breeding season. If a pulse of seeds became available to squirrels in the fall of 2001, and were cached and consumed over the following year, lower rates of nest predation would have resulted in 2002. Following low mast years, squirrels may have consumed alternate food items (bird eggs and nestlings), but then shifted to preferred items following high mast years (conifer seeds). Conifer seeds are preferred food items for red squirrels because they are an accessible, high nutrient food item that requires minimal search and handling time. Alternatively, higher squirrel survival following high mast years may have resulted in higher rates of nest predation; my measures of predator density may have been too imprecise to observe a numerical change. In Coastal Western Hemlock (CWH) forests on Haida Gwaii, British Columbia, a system similar to Interior Cedar-Hemlock (ICH) forests, red squirrel densities fluctuated with spruce cone production (Martin and Joron 2003). These findings suggest that even minor tree species within stands may exert an influence on the condition or quality of habitat for predators.

Changes in the foraging pattern of chickadees may be the result of annual variation in prey abundance and type. The dominant pattern of foraging for chestnut-backed chickadees within my study area was to glean arthropods from the foliage of mature trees at heights > 10 m. Chickadees foraging within the canopy typically gleaned

defoliators like western hemlock looper (*Lambdina fiscellaria lugubrosa*), green-striped forest looper (*Melanolophia imitata*), and spiders (Family Linyphiidae, Dictynidae, Philodromidae) from western hemlock trees (C. L. Mahon, personal observation; M. Schwarzfeld, University of Victoria, unpublished data). In 2001 this pattern of foraging was consistent among all sites possibly as a result of outbreak levels of defoliators. I observed the larvae of western hemlock looper and green-striped forest looper feeding on foliage during the late spring and dropping to the forest floor during the late summer of 2001 (C. L. Mahon, personal observation). In 2002, chestnut-backed chickadees increased their use of gap openings and foraged in tall and low shrub vegetation layers (intermediate, suppressed, and regenerating conifers, deciduous saplings and shrubs) at heights < 10 m.

These results suggest that chestnut-backed chickadees increased their use of understory vegetation for foraging in 2002 possibly due to (1) a decline in canopy defoliators associated with the dominant tree species, western hemlock, and/or (2) an outbreak of the two-year-cycle budworm (*Choristoneura biennis*), a defoliator associated with understory species in the ICH. Although it can be difficult to separate the effects of food abundance and predation on reproductive output, nest predation was the primary cause of nest failure in this system. If the loss of canopy defoliators had a major influence on reproductive output of chestnut-backed chickadees, I would have expected higher rates of nest failure due to abandonment or hatch failure, and lower productivity in 2002 (i.e., when rates of nest predation were low). While I was unable to assess how changes in prey availability altered foraging performance (e.g., prey delivery rates, total biomass per hour per chick) and reproductive output directly, my results suggest that chestnut-backed chickadees were able to exploit alternate foraging locations and provide

food to nestlings at all sites in 2002. Chestnut-backed chickadees appeared to adjust their use of prey when the abundance and type of prey changed. This is consistent with what is known about the foraging behaviour of conifer-associated chickadees; they are opportunistic foragers that use a wide variety of prey items during the breeding season (Grundel and Dahlsten 1991, Kleintjes and Dahlsten 1994, 1995). Studies of prey selection and foraging patterns found that great tits (*Parus major*) switched between prey types (spiders to caterpillars) to maximize prey sizes and nestling growth rate (Naef-Daenzer et al. 2000). Adult blue tits and great tits maximized their foraging performance when caterpillars were both abundant and large (Naef-Daenzer and Keller 1999). Blue tits can also adjust their foraging effort in different habitat types; adults in poor habitats had lower feeding rates and higher mean travel distances, but delivered prey that was 73% larger resulting in no difference in total biomass per hour per chick between rich and poor habitats (Tremblay et al. 2005). Thus, both *Poecile* and *Parus* species exhibit flexibility in their use of prey and compensatory behaviour when habitat or temporal effects change the abundance and diversity of prey types.

Future studies could assess the link between food supply and foraging patterns by quantifying prey abundance (e.g., frass-traps, pitfall traps, counts of bud damage), foraging effort or performance (travelling distance, prey delivery rates, proportion of optimal prey, total biomass per hour per chick), and the identity and size of prey delivered to chicks (Tremblay et al. 2005). Relationships between foraging patterns and reproductive output could be assessed by measuring not only nest success and productivity, but also nestling growth rate and fledging weight. Examining the influence of habitat diversity (e.g., number and proportion of habitat types with forest stands) on prey abundance, foraging performance, and prey size in each year can reveal if habitat

effects interact with temporal factors (Löhms 2003). The vegetation diversity within natural or harvested gap openings found within my 8 study sites could benefit insectivorous forest birds by providing alternate prey in years when dominant prey items (e.g., canopy arthropods) may be limited. Higher plant and arthropod species diversity may result in a higher number and frequency of insect outbreaks. Outbreak events occurring for multiple prey species may result in continuous pulses of food and a stable food supply for insectivorous birds.

My analyses of nest patch and nest tree attributes and nest success revealed few differences between successful and unsuccessful nests. Although chestnut-backed chickadees in most sites selected nest patches with higher densities of broken-top trees, nest success in these patches was lower. These results suggest that red squirrels may have used the characteristics of nest patches to direct their search (Martin 1993). I observed red squirrels investigating broken top trees containing cavities in multiple sites. The disconnect between the habitat attributes chosen for nest sites and those that predicted nest success may be due to temporal or spatial variation in selective pressures (Clark and Shutler 1999, Chase 2002). For chestnut-backed chickadees, a nest site may be safe in a year when predation risk is low, but unsafe in a year when predation risk is high. If chickadees cannot assess year-to-year changes in predation risk, then they may be vulnerable to changes in the environment that alter the relationship between the attractiveness of the habitat and its actual quality (Kristan 2003). Using a variety of nest site types may be a response to variable but high predation pressure in this system; under high nest predation, selection should favour those species that use a high diversity of nest sites (Willson and Gende 2000).

Changes in breeding territory characteristics had a stronger influence on chickadee nest success and behaviour. Annual differences in predator pressure resulting from short-term changes in resource availability for squirrels appeared to have the largest influence on chickadee reproductive output in my system. Changes in prey abundance and type between years, as indicated by foraging patterns of chestnut-backed chickadees, did not appear to influence reproductive output. The presence of pulsed resources in my system resulted in impacts on chestnut-backed chickadees that were both negative (e.g., indirect effects on predator-prey relationship) and positive (e.g., direct effects on insect abundance). Temporal changes in the availability of resources in this system resulted in strong annual variation in chickadee nest predation rates, foraging patterns, and productivity.

Table 4.1. Cover of vegetation layers within uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2002.

| Study site | n^b | Harvest ^c | % Tree | % High shrub ^d | % Low shrub ^e |
|------------------------|-------|----------------------|--------|------------------------------|-----------------------------|
| Uncut | | | | | |
| C1 | 12 | 0 | 55.4 | 4.2 | 1.9 |
| HL7 | 13 | 0 | 46.4 | 7.9 | 6.0 |
| D3 ^a | 12 | 0 | 44.2 | 12.3 | 25.1 |
| Partial cut- mature | | | | | |
| C3 | 8 | 30 | 24.6 | 6.8 | 25.0 |
| HL5 | 12 | 40 | 24.6 | 7.5 | 18.7 |
| C2 | 12 | 60 | 24.4 | 7.8 | 19.2 |
| Partial cut-old | | | | | |
| D5 ^a | 8 | 30 | 36.8 | 3.4 | 21.9 |
| D4 ^a | 12 | 60 | 17.7 | 8.3 | 19.3 |

^aStand age--old growth (353-373 years). For all other sites, stand age--mature (145 years).

^bNumber of random plots (n) sampled in each site during 2000-2002.

^cHarvest was approximate % volume removal.

^dHigh shrubs include all woody plants 2-10 m tall.

^eLow shrubs include all woody plants < 2 m tall.

Table 4.2. Habitat structure in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2002. Density is presented as stems/0.031 ha plots.

| | | All trees | | Dead trees | | Diseased trees | | Tall shrubs/ saplings ^c | |
|------------------------|-----------------------|-----------|-----|------------|-----|----------------|-----|---------------------------------------|------|
| Study site | <i>n</i> ^b | <i>x</i> | SE | <i>x</i> | SE | <i>x</i> | SE | <i>x</i> | SE |
| Uncut | | | | | | | | | |
| C1 | 12 | 42.5 | 3.7 | 7.0 | 0.9 | 18.6 | 2.1 | 134.2 | 7.4 |
| HL7 | 13 | 29.2 | 3.1 | 4.2 | 0.7 | 18.0 | 1.8 | 152.1 | 7.4 |
| D3 ^a | 12 | 23.0 | 2.7 | 4.4 | 0.6 | 15.6 | 1.5 | 201.6 | 12.7 |
| Partial cut- mature | | | | | | | | | |
| C3 | 8 | 17.5 | 2.1 | 5.0 | 0.6 | 10.9 | 2.1 | 195.9 | 11.4 |
| HL5 | 12 | 18.3 | 2.5 | 3.2 | 0.6 | 8.8 | 1.2 | 146.3 | 18.4 |
| C2 | 12 | 18.9 | 2.1 | 2.8 | 0.5 | 8.2 | 1.1 | 182.7 | 16.4 |
| Partial cut-old | | | | | | | | | |
| D5 ^a | 8 | 15.0 | 2.7 | 2.2 | 0.4 | 10.1 | 2.5 | 178.8 | 17.5 |
| D4 ^a | 12 | 9.8 | 1.3 | 1.0 | 0.0 | 7.1 | 1.4 | 164.3 | 20.8 |

^aStand age--old growth (353-373 years). For all other sites, stand age--mature (145 years).

^bNumber of random plots (*n*) sampled in each site during 2000-2002.

^cTall shrubs/saplings were woody plants < 12.5 cm DBH.

Table 4.3. Daily mortality rate (DMR) and average number of young fledged for chestnut-backed chickadees in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia.

| Study site | 2001 | | | 2002 | | | 2003 | | |
|--------------------|-----------------------|------------------|---------------|----------|-------|---------------|----------|-------|---------------|
| | <i>n</i> ^b | DMR ^c | Young fledged | <i>n</i> | DMR | Young fledged | <i>n</i> | DMR | Young fledged |
| Uncut | | | | | | | | | |
| C1 | 1 | 0.061 | 0 | -- | | | 1 | 0 | 4.0 |
| HL7 | 4 | 0.029 | 0.5 | 3 | 0.053 | 0 | 2 | 0.017 | 2.5 |
| D3 ^a | 3 | 0.039 | 0 | 3 | 0 | 2.7 | 1 | 0 | 6.0 |
| Partial cut-mature | | | | | | | | | |
| C3 | 4 | 0.042 | 0 | 2 | 0.011 | 1.5 | 2 | 0.021 | 3.0 |
| HL5 | 2 | 0.057 | 0 | 5 | 0 | 3.0 | 4 | 0 | 4.0 |
| C2 | 1 | 0 | 4.0 | 2 | 0 | 3.0 | 3 | 0 | 3.7 |
| Partial cut-old | | | | | | | | | |
| D5 ^a | 4 | 0.024 | 1.0 | 2 | 0.024 | 0 | 1 | 0.222 | 0 |
| D4 ^a | 3 | 0.042 | 0 | 4 | 0 | 3.2 | 3 | 0.037 | 0.7 |

^aStand age--old growth (353-373 years). For all other sites, stand age--mature (145 years).

^b*n* was the number of nests.

^cDaily mortality rate (DMR) was the number of failed nests divided by the total number of exposure days.

Table 4.4. Predator daily mortality rate (PDMR) and percent nests depredated for chestnut-backed chickadees in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia.

| Study site | 2001 | | | 2002 | | | 2003 | | |
|--------------------|-------|-------------------|--------------------|------|-------|--------------------|------|-------|--------------------|
| | n^b | PDMR ^c | % | n | PDMR | % | n | PDMR | % |
| | | | Nests ^d | | | Nests ^d | | | Nests ^d |
| Uncut | | | | | | | | | |
| C1 | 1 | 0.061 | 87.3 | -- | | | 1 | 0 | 0 |
| HL7 | 4 | 0.019 | 47.3 | 3 | 0 | 0 | 2 | 0 | 0 |
| D3 ^a | 3 | 0.026 | 58.0 | 3 | 0 | 0 | 1 | 0 | 0 |
| Partial cut-mature | | | | | | | | | |
| C3 | 4 | 0.042 | 75.6 | 2 | 0.011 | 31.3 | 2 | 0 | 0 |
| HL5 | 2 | 0.029 | 61.6 | 5 | 0 | 0 | 4 | 0 | 0 |
| C2 | 1 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 0 |
| Partial cut-old | | | | | | | | | |
| D5 ^a | 4 | 0.024 | 55.9 | 2 | 0.012 | 33.1 | 1 | 0.22 | 99.9 |
| D4 ^a | 3 | 0.021 | 50.1 | 4 | 0 | 13.8 | 3 | 0.019 | 46.3 |

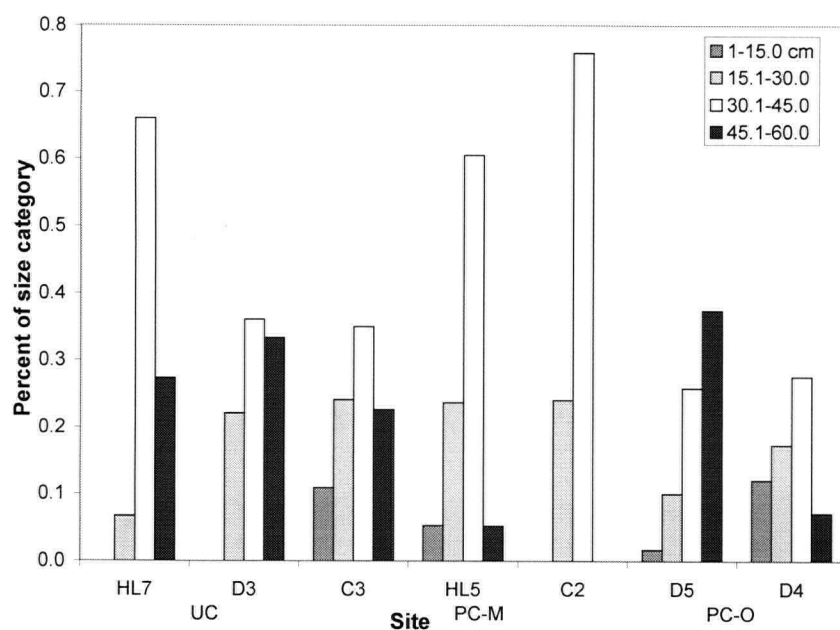
^aStand age--old growth (353-373 years). For all other sites, stand age--mature (145 years).

^b n was the number of nests.

^cPredator daily mortality rate (DMR) was the number of nests destroyed by a predator divided by the total number of exposure days.

^dPercent nests depredated (PDMR) was the proportion of nests depredated when extrapolating the PDMR to a 33 day nesting cycle. Calculated as $(1 - \text{PDMR})^d$, where d is the number of days in the nesting cycle (incubation and nestling period = 33 days for chestnut-backed chickadees).

A.



B.

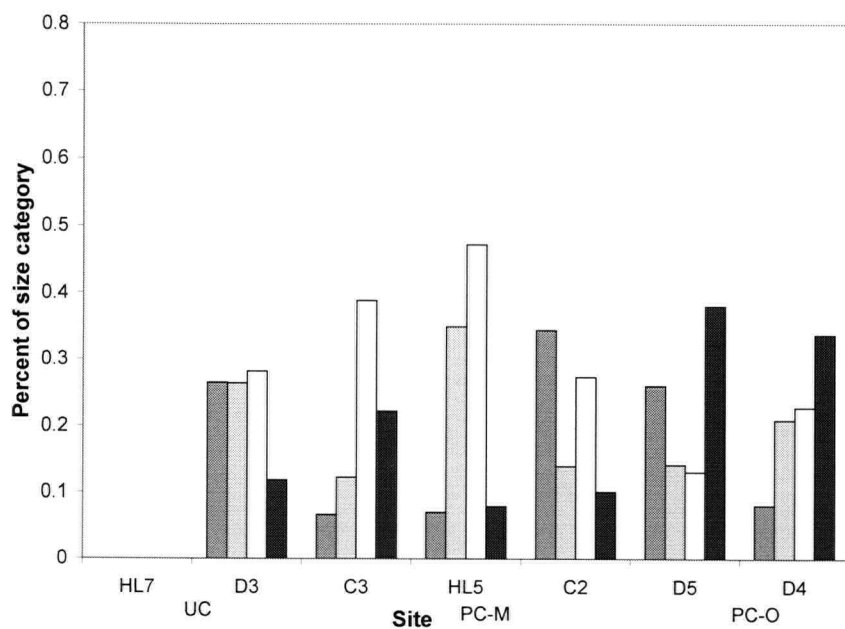
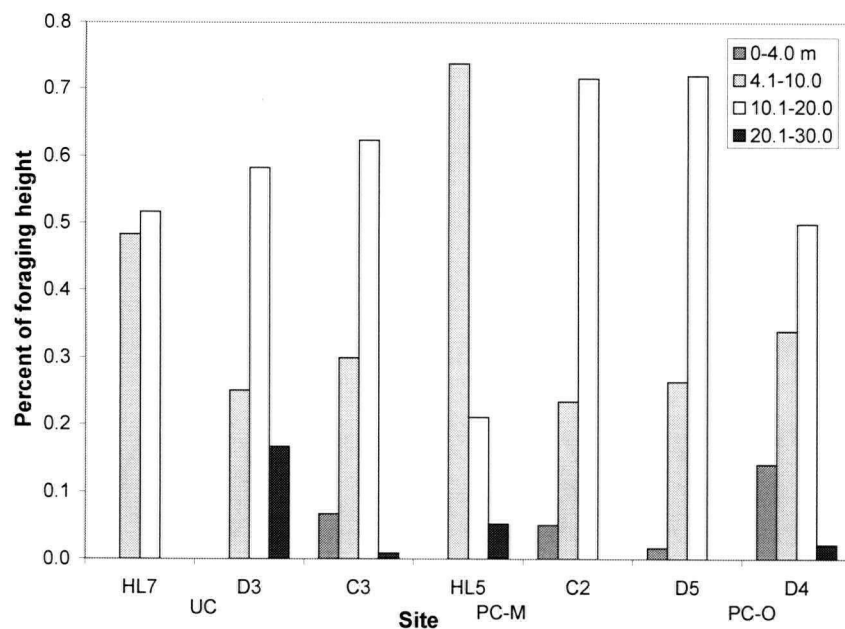


Figure 4.1. Vegetation sizes (diameter at breast height) used by foraging chestnut-backed chickadees at McCully Creek, British Columbia in 2001 (A) and 2002 (B). Uncut sites = HL7, D3; Partial cut-mature (PC-M) sites = C3, HL5, C2; Partial cut-old (PC-O) sites = D5, D4.

A.



B.

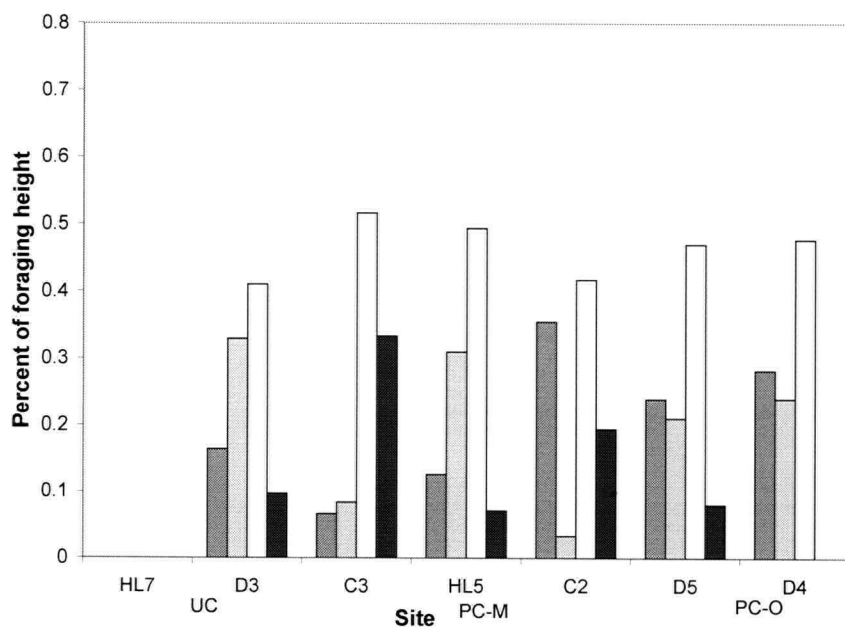
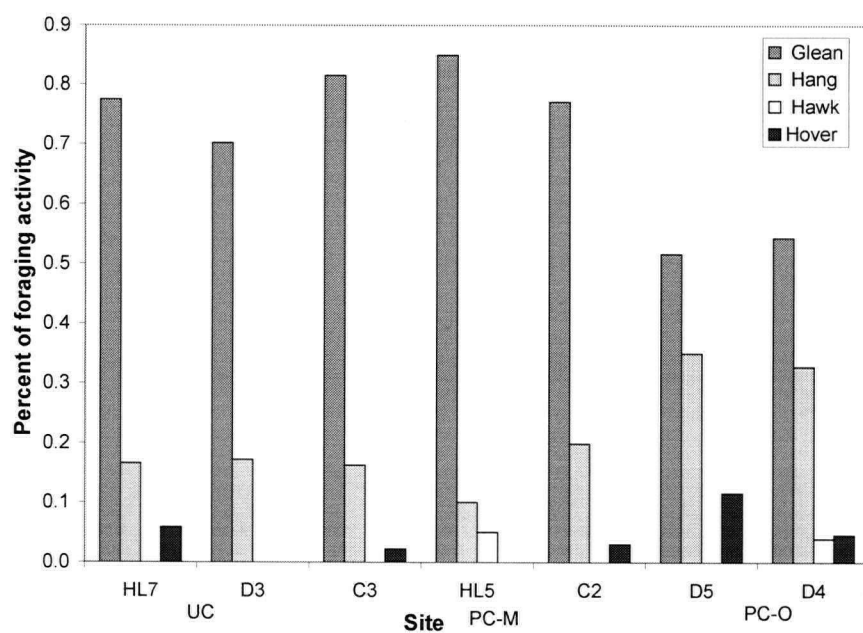


Figure 4.2. Vegetation heights used by foraging chestnut-backed chickadees at McCully Creek, British Columbia in 2001 (A) and 2002 (B). Uncut sites = HL7, D3; Partial cut-mature (PC-M) sites = C3, HL5, C2; Partial cut-old (PC-O) sites = D5, D4.

A.



B.

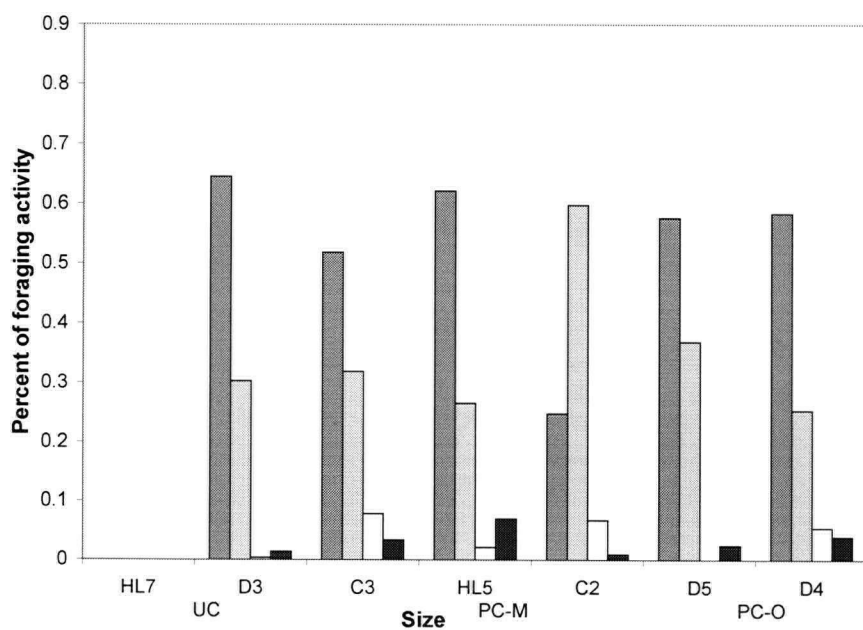


Figure 4.3. Foraging activities used by chestnut-backed chickadees at McCully Creek, British Columbia in 2001 (A) and 2002 (B). Uncut sites = HL7, D3; Partial cut-mature (PC-M) sites = C3, HL5, C2; Partial cut-old (PC-O) sites = D5, D4.

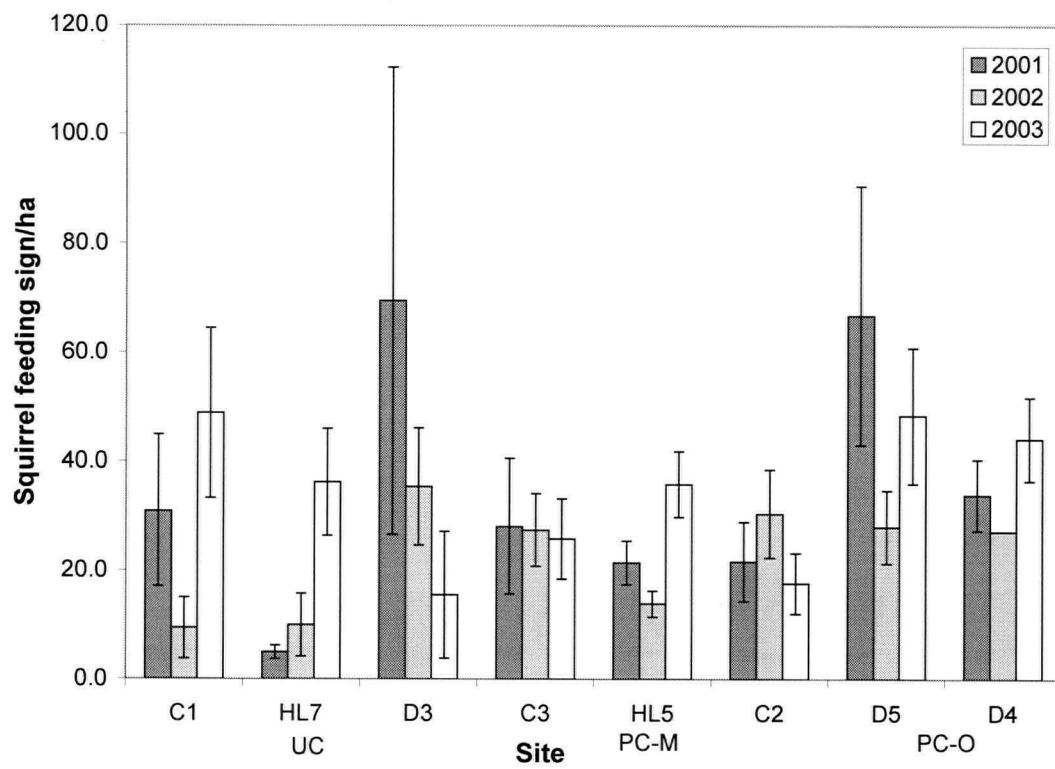


Figure 4.4. Index of predator density (squirrel feeding sign/ha) at each site at McCully Creek, British Columbia, 2001-2003.

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CHAPTER 5:

CONCLUSIONS

Temporal Variation and Community Interactions

Many terrestrial systems are characterized by pulsed resources, the short-term availability of high levels of resources that become depleted with time (Ostfeld and Keesing 2000). Fluctuations in resource availability can result in temporal variability in the density, habitat use, and demography (reproduction, survival) of bird and mammal populations. This study emphasized the value of (1) following populations for multiple years to observe year by habitat interactions, and (2) understanding interactions among birds, their predators, and the environment. I observed annual variation in chestnut-backed chickadee (*Poecile rufescens*) nest predation rates, foraging patterns, and productivity possibly due to fluctuations in the availability of resources for chickadees and their main predator, the red squirrel (*Tamiasciurus hudsonicus*).

All birds selecting breeding territories face a complex forecasting problem; they use environmental cues when a habitat choice is made to assess the quality of a site to be used at some later time. As a result, birds are vulnerable to spatial or temporal changes in the environment that alter the relationship between the attractiveness of the habitat and its actual quality (Kristan 2003). When temporal variation in resources (for birds or predators) influences the quality of habitat, species may have less success selecting habitats that consistently result in high reproductive success and survival. A short-term study (1-2 years) may have concluded that all sites within McCully Creek (mature and old, uncut and partial cut) were sink habitats (Pulliam 1988, Donovan et al. 1995) or ecological traps (Donovan and Thompson 2001, Bayne and Hobson 2002).

Annual variation in chestnut-backed chickadee foraging patterns may have been caused by short-term changes in food supply. Regional or global climatic fluctuations like El Niño southern-oscillation (ENSO) events have been linked to higher arthropod biomass in temperate deciduous forests (Sillet et al. 2000, Holmes and Sherry 2001). Outbreaks of defoliating caterpillars (Lepidoptera) have elicited both numerical (Holmes et al. 1986, Holmes and Sherry 2001, Jones et al. 2003) and functional responses (Connor et al. 1999, Tremblay et al. 2003) in forest birds. Pulses of caterpillars have also increased the reproductive output (number of young fledged) of insectivorous forest birds (Sillet et al. 2000, Tremblay et al. 2003).

Within my study area, chestnut-backed chickadees foraged on looper larvae that defoliated the canopy foliage of hemlock, and small budworm larvae that attacked the developing buds of regenerating fir found in the understory and gap openings of mature and old stands. Although chestnut-backed chickadees are predominantly canopy gleaners (Airola and Barrett 1985, Weikel and Hayes 1999, Dahlsten et al. 2002), I observed chickadees use alternate foraging activities (e.g., hanging) and forage at a variety of heights in different vegetation layers in order to exploit outbreaks of both looper (2001) and budworm (2002). Chestnut-backed chickadees may need to select territories that allow them to take advantage of spatial and temporal changes in prey availability. In one year, the amount of canopy foliage may result in high prey availability within a territory, while in another year, the amount of understory foliage (intermediate, suppressed, regenerating trees, high shrub layer) may result in high prey availability. The ability of chickadees to take advantage of short-term changes in the spatial distribution of their prey (Robinson and Holmes 1982), may have allowed them to successfully occupy the structurally diverse, temporally variable forest sites at McCully Creek.

My findings suggest that complex ecological factors, as opposed to only habitat factors, strongly influenced the reproductive success of chestnut-backed chickadees at McCully Creek. Contrary to my expectations, harvest treatment, nest patch variables, and predator proximity did not influence the nest survival of chickadees. Nest height was the only habitat-related variable (nest tree scale) that influenced nest survival. Indices of predator density (stand scale), also weakly influenced nest survival. Chestnut-backed chickadee nest survival appeared to be most influenced by regional environmental cues that caused annual fluctuations in resources (e.g., conifer seeds) for red squirrels. Annual rainfall and mean temperature during the growing season are environmental variables that have been correlated with annual seed production (Sork et al. 1993, Woodward et al. 1994) and both are suspected to be uniform over large geographic areas (Norton and Kelly 1988). Recent evidence for 10 genera of Northern Hemisphere trees suggests that temporal patterns of seed production were not correlated with annual rainfall or mean summer temperature, although spatial patterns of seed production and environmental variables were similar, with both exhibiting large-scale spatial synchrony (Koenig and Knops 2000). Spatial autocorrelation might be expected if environmental cues synchronize growth and reproduction, although the absence of consistent temporal autocorrelation suggests that annual seed production may be an evolved strategy whereby tree species switch between growth (small seed crops) and reproduction (large seed crops), instead of responding directly to annual environmental variability ("resource matching").

Regardless of the mechanism that produces large seed crops, these pulsed resources have important implications for bird and mammal populations that depend on the seeds of forest trees for food (Bock and Lepthien 1976, Hannon et al. 1987, McShea

2000). Populations of resident species dependent on mast may be affected synchronously over large geographic areas by both bumper crops and crop failures (Koenig and Knops 2000). In addition, the cascading effects of annual seed production may result in direct and indirect effects on ecosystem structure and function. In temperate oak forests, masting acorn crops increased mouse and chipmunk abundance (Ostfeld et al. 1996, McShea 2000), but also nest predation rates on forest songbirds (Schmidt et al. 2001, Schmidt 2003, Schmidt and Ostfeld 2003). In my system, pulsed resources in the form of conifer seeds may have been an unstable, temporally variable food supply for red squirrels. Squirrels may have exhibited a functional response to changes in their food supply by switching to alternate prey items (bird eggs and nestlings) during periods of low seed production. In Coastal Western Hemlock (CWH) forests on Haida Gwaii (Queen Charlotte Islands, British Columbia), red squirrels exhibited a numerical response to changes in spruce cone production causing nest predation rates on forest songbirds to fluctuate annually (Martin and Joron 2003).

My study emphasized the importance of considering interactions among birds, their predators, and the environment and the need to examine both patterns and mechanisms of nest predation. Although many studies have examined nest predation in relation to habitat at various scales (for a review, see Chalfoun et al. 2002), relatively few have examined the process of nest predation as an interaction between predator and prey (Schmidt 1999, Schmidt et al. 2001, Schmidt and Ostfeld 2003). My work also emphasized the role of red squirrels in forest food webs. Red squirrels may play a central role in conifer-dominated, temperate forests by exhibiting population fluctuations in response to changes in conifer seed supply (Kemp and Keith 1970, Rusch and Reeder 1978, Wheatley et al. 2002), reducing the reproductive success of a variety of forest

songbird species (Martin 1993, Sieving and Willson 1998, Tewksbury et al. 1998, Martin and Joron 2003), including weak cavity excavators (this study), and reducing the reproductive success of forest-dwelling raptors like the northern goshawk (*Accipiter gentilis*). Low squirrel numbers after mast failure events may lower the breeding condition of female goshawks resulting in aborted or failed breeding attempts in northwest British Columbia (T. E. Mahon, unpublished data). In western Washington, declines in prey abundance following an El Niño winter (higher precipitation and lower temperatures) altered northern goshawk space use, reproduction, and survival. Goshawk home range size more than doubled, while mean number fledged per occupied territory declined by 94%, and annual survival rates of adult goshawk were reduced by 36% (Bloxtton 2002).

Habitat Use and Selection at Multiple Scales

My results suggest that chestnut-backed chickadees at McCully Creek responded to both coarse and fine-grained habitat variables. At the stand scale, I found chickadees at similar densities in uncut, partial cut-mature, and partial cut-old treatments. Chickadee breeding density was not related to the structural characteristics of stands in my study area, suggesting that the density of trees left behind after partial cutting did not limit chickadees from establishing and using breeding territories in uncut and partial cut stands. Insectivorous birds may use the amount of above-ground foliage density to assess the availability of foraging habitat (and caterpillar density) within a potential territory (Marshall and Cooper 2004). Chickadees breeding at McCully Creek may need to assess both the amount of canopy foliage and the amount of high shrub cover when selecting a territory due to annual changes in insect type and abundance. Territories that contain a variety of habitat types (closed canopy forest, forest gaps, forest edge) may increase

foraging opportunities for chickadees by providing a wide variety of substrates and prey species, and alternate foraging habitats when levels of primary prey (canopy defoliating arthropods) are low.

Chickadees selected fine-grained habitat variables at the nest patch and nest tree scales (e.g., trees with broken tops and boring insects) suggesting the importance of these attributes for this species. Like all weak cavity excavators, chickadees require nest trees with soft, decayed wood (Smith 1991, Albano 1992, Martin et al. 2004). Stands without diseased, broken top, or insect-attacked trees, will not meet the breeding requirements of this species because small body and bill size prevents chickadees and nuthatches from excavating cavities in sound wood. Because chestnut-backed chickadees are small, they can use areas of localized damage and insect attack that softens heartwood in a section of a living tree. These attributes were found in a variety of tree species and in a wide range of tree conditions within uncut and partial cut sites at McCully Creek. As a result, chestnut-backed chickadees could locate their nests in live trees with small areas of damage (e.g., branch holes, wound sites, cracks, bark beetle attack) or in dying or dead trees in an advanced stage of decay (e.g., broken top, root or stem rot, wood-boring beetle attack).

Resistance to Habitat Change

At the landscape scale, the response of forest birds to fragmentation (decreases in patch size and increases in amount of edge and in patch isolation) resulting from forest harvesting have been minimal or not-observed (Schmiegelow et al. 1997, Trzcinski et al. 1999, Donovan and Flather 2002, Schmiegelow and Mönkkönen 2002). In general, forest birds exhibit few responses to biological and physical edge effects, do not avoid edge habitats, and show inconsistent patch size or isolation effects (for a review, see

Schmiegelow and Mönkkönen 2002). At the stand scale, the response of forest birds to harvesting depends on species-specific habitat requirements (habitat types and attributes), and the type and intensity of harvesting procedures. At McCully Creek, chestnut-backed chickadees showed resistance to habitat change created by low to high intensity partial cut harvesting. Birds inhabiting forest types dominated by small-scale disturbances may be resistant to small and large openings in the canopy created by harvesting because these simulate the natural disturbance events (wind, insects, disease) operating within these stands (Steventon et al. 1998, Chambers et al. 1999, Robinson and Robinson 1999, Leupin et al. 2004). Chestnut-backed chickadees were able to use nest sites and foraging areas within the intermediate level of disturbance created by partial cutting because characteristics of mature and old forests were maintained (e.g., suitable nest trees), but in addition, new habitat types were created due to increased spatial and structural diversity within stands. Partial cutting created a mosaic of habitat types within stands including uncut and thinned forest, forest gaps, and forest edge. Use of partial cut sites by chestnut-backed chickadee may be linked to the maintenance of a sufficient supply of edge habitats, and specific habitat features (large trees with disease, insects, damage) associated with mature and old forests.

Partial cutting results in edge habitat dispersed throughout harvested sites—at the interface between uncut or thinned forest and gap openings, trails, roads, and landings. At McCully Creek, partial cut sites were completely permeated by edge that birds could not avoid if they held territories within the site. Although edge effects have been linked to increased rates of songbird nest predation (for a review, see Paton 1994 and Lahti 2001), evidence of a negative edge effect at forest-clearcut edges is inconsistent (for a review, see Schmiegelow and Mönkkönen 2002). More recent evidence suggests that

patterns of nest predation are likely influenced by landscape context (Tewksbury et al. 1998), the predator community (Schmidt et al. 2001), and the responses (numerical and functional) of the predator (Chalfoun et al. 2002, Schmidt and Ostfeld 2003) as opposed to habitat characteristics alone.

Environmental conditions can also change due to increased amounts of edge habitat. Physical edge effects may include an increased amount of sunlight, wind, temperature variation, and other microclimate changes (Matlack 1994, Chen et al. 1995). In partial cut sites within ICH forests, the presence of both edge and gap habitats likely resulted in higher structural and species diversity of understory vegetation. In addition, increased light and space at edges may have increased invertebrate diversity (e.g., shade-intolerant species), while higher vegetation diversity and diverse microclimates may have increased the abundance of invertebrates (Chen et al. 1992, Matlack 1994, Jokimäki 1998, Shure and Phillips 1991). Chestnut-backed chickadees in all sites (uncut and partial cut) used a high proportion of edge habitats when foraging, suggesting that natural and anthropogenic edges in this system may have provided higher food abundance. Chickadees also foraged in the early seral vegetation found within gap openings (regenerating conifers, deciduous saplings and shrubs). Higher vegetation diversity in gap openings may have provided alternate prey in years when dominant prey items (e.g., canopy arthropods) were limited.

At McCully Creek, both mature and old partial cut sites provided breeding habitats for chestnut-backed chickadees possibly because they provided chickadees with (1) an abundant supply of specific attributes, and (2) stands that retained trees in high enough densities to mimic natural gap creation events. These attributes included large trees with high amounts of above-ground biomass, trees with evidence of disease or

insect attack (stem and root disease, boring insects, defoliating insects, mistletoe) and damage (broken tops, branch holes, wound sites), and a diversity of habitat types (uncut and thinned forest, forest gaps, forest edge, riparian and wetland areas). At the Date Creek experimental forest within the ICH, partial cut harvest levels up to 60% tree volume removal maintained most bird species associated with mature forests, while clearcuts with retention of mature deciduous species did not (Steventon et al. 1998). Types of harvesting systems that remove > 60% tree volume may also provide suitable habitat for mature forest species, although the appearance of these stands with respect to tree densities and the spatial arrangement of trees may differ substantially from partial cut stands (e.g., variable retention, clearcut with reserves). The size of tree species removed during harvesting (across the size range of tree species found within the stand or a restricted size range—mid or large diameter trees only) may also influence the suitability of stands because larger, older trees can have different characteristics (e.g., shape, structure, amount of biomass, decay stage, disease susceptibility) than smaller, younger trees. Large cavity nesting species like woodpeckers and large raptors (owls, hawks, eagles) require large trees for nesting. For chestnut-backed chickadees, mature and old partial cut stands in the ICH provided suitable nest sites in close proximity to favourable foraging habitat. Partial cutting retained structural features (standing dying or dead trees) used as nesting habitat but also created stands that simulated small-scale gap creation events (Steventon et al. 1998, Chambers et al. 1999, Leupin et al. 2004).

Cavity nester populations that depend on dying or dead trees for nest sites may be limited by the availability of suitable nest trees in managed forests (Brawn and Balda 1988, Newton 1994, Dobkin et al. 1995). The loss of diseased or dying trees found in mature and old forests may not currently be a concern for forest managers in Canada

because harvesting in most regions is still in the first rotation. Many forest landscapes remain dominated by mature and old forests which may buffer local impacts of habitat loss and fragmentation resulting from forest harvesting (Schmiegelow et al. 1997). As harvesting continues within the McCully Creek watershed, the seral stage and species composition of stands will change. It is the loss of standing diseased, damaged, and dead trees from regenerating forests/second growth forests that may negatively effect cavity nesters. The type of harvesting activity can also influence the availability of suitable nest trees. At McCully Creek, trees were removed across all species and diameter classes. Removing only small diameter trees may provide high numbers of large, diseased, damaged, and dying trees in the short-term, but may limit the future recruitment of these trees. Removing only large diameter trees may reduce the availability of suitable nest trees in the short-term and possibly the long-term, depending on the time it takes for individual tree species to acquire attributes that increase their suitability as nest trees. Retention of both mature and old trees will maintain suitable nest trees during the transition from early to late seral stage forest. Stands that maintain conifer and deciduous species found in the canopy layer, across the size ranges and health conditions that occur within the stand may provide the most suitable habitat for cavity nesting birds.

Landscape-scale studies examining effects of habitat loss on forest birds suggest negative impacts for resident species associated with old boreal forests (Schmiegelow et al. 1997, Hejl et al. 2002, Schmiegelow and Mönkkönen 2002). Cavity nesting species like the boreal chickadee (*Poecile hudsonicus*) and three-toed woodpecker (*Picoides tridactylus*) are resident species thought to be threatened by changes in the boreal forest in Canada (Imbeau et al. 2001, Schmiegelow and Mönkkönen 2002). Future intensive harvesting of old boreal forests (conversion to early seral stages at a rate that exceeds

natural disturbance patterns), permanent habitat loss (conversion to industrial or agricultural uses), and fragmentation (linear features like pipelines and roads) could result in declines for these species that mirror significant population declines of woodpecker species in Fennoscandia (Finnish and Swedish forest landscapes) following centuries of agriculture and timber harvesting activities (Angelstam and Mikusinski 1994, Imbeau et al. 2001). My study suggests the need to consider stand-scale variables like harvest type and intensity in larger landscape-scale studies of habitat loss. Negative impacts associated with loss of forest habitat could be mitigated by the use of alternative harvesting systems like partial cutting. In addition, researchers should consider the type of disturbance agents operating within forest systems when assessing potential impacts of harvesting on forest-dwelling species. Species associated with forest types dominated by small-scale disturbances may exhibit fewer responses (good resistance) to less-intensive harvesting procedures (e.g., partial cutting), but greater responses to intensive harvesting (e.g., clearcut with reserves). Hejl et al. (2002) suggested that old-growth cedar/hemlock stands represent moist forest types that form homogeneous landscapes and that species like chestnut-backed chickadees would be negatively affected by harvesting in these forest types. While the term homogeneous may describe the landscape scale pattern of these forests (i.e., contiguous areas of old forest), at the stand scale ICH forests are heterogeneous and contain a mosaic of habitat types including closed canopy forest, small and large forest gaps, and forest edge (Coates and Burton 1997). Chickadees at McCully Creek benefited from this heterogeneity by selecting a diversity of nest sites and using a variety of habitat types for foraging within both uncut and partial cut sites. Both the scale and intensity of harvesting activities should be considered by forest managers hoping to maintain structural characteristics associated with mature and old forest stands.

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APPENDIX I. The relationship between nest patch (A), nest tree (B), and nest placement habitat variables (C) and chestnut-backed chickadee nest success ($n = 57$ nests) as predicted by logistic regression, 2000-2003.

| Habitat variable | <i>B</i> | SE | Wald <i>T</i> | <i>P</i> | Odds ratio | 95% CI L | 95% CI U |
|---------------------------|----------|-------|---------------|----------|------------|-------------|-------------|
| A. Nest patch | | | | | | | |
| Tree cover | -1.31 | 1.80 | 0.54 | 0.464 | 0.27 | 0.01 | 9.06 |
| Shrub cover | -2.25 | 1.48 | 2.32 | 0.128* | 0.11 | 0.01 | 1.91 |
| All trees | -0.001 | 0.02 | 0.001 | 0.977 | 0.99 | 0.96 | 1.04 |
| Dead trees | -0.09 | 0.08 | 1.13 | 0.288 | 0.92 | 0.78 | 1.08 |
| Diseased trees | -0.02 | 0.04 | 0.39 | 0.534 | 0.98 | 0.91 | 1.05 |
| Average DBH | -0.03 | 0.03 | 1.00 | 0.316 | 0.97 | 0.91 | 1.03 |
| Conks | -0.17 | 0.10 | 3.01 | 0.083* | 0.85 | 0.70 | 1.02 |
| Blind conks | -0.03 | 0.08 | 0.18 | 0.669 | 0.97 | 0.83 | 1.12 |
| Boring | | | | | | | |
| insects | -0.06 | 0.04 | 2.44 | 0.119* | 0.94 | 0.88 | 1.02 |
| Broken tops | -0.25 | 0.13 | 3.82 | 0.050* | 0.78 | 0.61 | 1.00 |
| Brown needles | 0.007 | 0.07 | 0.01 | 0.924 | 1.01 | 0.87 | 1.16 |
| Frost crack | -0.12 | 0.07 | 3.10 | 0.078* | 0.89 | 0.78 | 1.01 |
| Habitat type ^a | | | 0.34 | 0.952* | | | |
| Thinned forest | -0.08 | 0.60 | 0.02 | 0.895 | 0.92 | 0.28 | 3.00 |
| Harvest gap | 0.56 | 1.25 | 0.20 | 0.654 | 1.75 | 0.15 | 20.23 |
| Riparian | -8.74 | 34.89 | 0.06 | 0.802 | 0.00 | . | . |

| | | | | | | | |
|-----------------------------|-------|--------|------|--------|------|------|--------|
| B. Nest tree | | | | | | | |
| Tree species ^b | | | 3.08 | 0.878* | | | |
| Hw | -9.44 | 99.63 | 0.01 | 0.924 | 0.00 | . | . |
| Bl | -9.20 | 99.64 | 0.01 | 0.926 | 0.00 | . | . |
| Ep | -8.80 | 99.63 | 0.01 | 0.930 | 0.00 | . | . |
| At | -7.95 | 99.63 | 0.01 | 0.936 | 0.00 | . | . |
| Sx | 0.00 | 122.02 | 0.00 | 1.00 | 1.00 | 0.00 | 73.00 |
| Cw | -9.20 | 99.64 | 0.01 | 0.926 | 0.00 | . | . |
| Act | 0.00 | 111.39 | 0.00 | 1.00 | 1.00 | 0.00 | 65.00 |
| Live | 0.47 | 0.57 | 0.68 | 0.411 | 1.60 | 0.52 | 4.91 |
| Dead | -0.47 | 0.57 | 0.68 | 0.411 | 0.62 | 0.20 | 1.92 |
| Diseased | -6.87 | 25.92 | 0.07 | 0.791* | 0.00 | . | . |
| DBH | 0.001 | 0.01 | 0.01 | 0.915 | 1.00 | 0.98 | 1.03 |
| Conk | -0.32 | 0.54 | 0.36 | 0.551 | 0.72 | 0.25 | 2.09 |
| Blind conk | 0.86 | 0.56 | 2.41 | 0.121* | 2.37 | 0.80 | 7.08 |
| Boring insects ^c | | | 2.26 | 0.521 | | | |
| BI - 0 | 1.64 | 1.15 | 2.03 | 0.154 | 5.14 | 0.54 | 48.90 |
| BI - 1 | 0.54 | 0.95 | 0.32 | 0.571 | 1.71 | 0.27 | 11.06 |
| BI - 2 | 0.07 | 0.62 | 0.01 | 0.911 | 1.07 | 0.32 | 3.58 |
| Broken top | -0.27 | 0.56 | 0.24 | 0.627 | 0.76 | 0.25 | 2.28 |
| Brown needles | 0.32 | 1.26 | 0.06 | 0.800 | 1.38 | 0.12 | 16.11 |
| Frost crack | 0.56 | 0.55 | 1.04 | 0.307 | 1.75 | 0.60 | 5.12 |
| Wood condition ^d | | | 4.77 | 0.444 | | | |
| WC - 2 | 1.61 | 1.79 | 0.81 | 0.368 | 5.00 | 0.15 | 166.55 |
| WC - 3 | 0.29 | 1.48 | 0.04 | 0.846 | 1.33 | 0.07 | 24.32 |
| WC - 4 | 1.10 | 1.56 | 0.49 | 0.482 | 3.00 | 0.14 | 64.26 |
| WC - 5 | -0.56 | 1.55 | 0.13 | 0.718 | 0.57 | 0.03 | 11.85 |
| WC - 6 | 0.41 | 1.68 | 0.06 | 0.810 | 1.50 | 0.06 | 40.63 |
| C. Nest placement | | | | | | | |
| Nest height | 0.10 | 0.05 | 4.43 | 0.035* | 1.10 | 1.01 | 1.21 |
| Nest tree cover | -7.01 | 3.27 | 4.61 | 0.032* | 0.00 | 0.00 | 0.54 |

| | | | | | | | |
|----------------------------|-------|-------|------|-------|---------|------|--------|
| Nest position ^e | | | 0.29 | 0.866 | | | |
| Bole | -5.79 | 22.24 | 0.07 | 0.794 | 0.00 | . | . |
| Top | -6.20 | 22.26 | 0.08 | 0.781 | 0.00 | . | . |
| Cavity type ^f | | | 1.95 | 0.584 | | | |
| Natural | 6.39 | 22.24 | 0.08 | 0.774 | 598.15 | 0.00 | 5.1E21 |
| Secondary | 7.30 | 22.25 | 0.11 | 0.743 | 1477.78 | 0.00 | 1.3E22 |
| Primary | 6.42 | 22.25 | 0.08 | 0.773 | 615.74 | 0.00 | 5.3E21 |
| Cavity number | -0.12 | 0.17 | 0.46 | 0.495 | 0.89 | 0.64 | 1.24 |

*The nest patch variable habitat type ($\chi^2 = 5.99$, $df = 3$, $P = 0.112$) and the nest tree variables tree species ($\chi^2 = 11.27$, $df = 7$, $P = 0.127$) and diseased ($\chi^2 = 2.11$, $df = 1$, $P = 0.146$) each contributed to the model outcome ($P < 0.25$), but coefficients were not significant possibly due to small sample sizes and low power. I included these variables in multivariate models because univariate analyses were meant to serve as a preliminary, coarse-level analysis to determine which habitat variables influenced nest fate.

^aHabitat types were: (1) forest, (2) thinned forest, (3) harvest gap, (4) riparian.

^bTree species were: western hemlock (Hw), western redcedar (Cw), subalpine fir (Bl), amabilis fir (Ba), lodgepole pine (Pl), hybrid spruce (Sx), paper birch (Ep), trembling aspen (At), and black cottonwood (Act).

^cBeetle infestation levels were categorized by the number of exit holes : (0) 0, (1) < 5, (2) 5 - 30, (3) 30 +

^dWood condition was (1) no decay, (2) probably limited decay, (3) wood essentially hard; limited decay, (4) wood mostly hard but soft wood present, (5) hard and soft wood; spongy sections, (6) soft and spongy wood, (7) soft and spongy; powdery sections.

^eNest position was (1) bole, (2) top, (3) branch.

^fCavity type was (1) natural, (2) primary, (3) secondary, (4) unknown.

APPENDIX II. Distribution of forest health agents among tree species at random sampling sites in uncut, partial cut-mature, and partial cut-old sites at McCully Creek, British Columbia, 2000-2002.

| Study site | Tree species | Total trees | Stem rot | | | Boring insects | | | Broken top | | |
|----------------|--------------|-------------|-----------------------|--------------------|--------------------|----------------|-------|-------|------------|-------|-------|
| | | | <i>n</i> ^a | % - S ^b | % - T ^c | <i>n</i> | % - S | % - T | <i>n</i> | % - S | % - T |
| UC | | | | | | | | | | | |
| C1 | Hw | 337 | 43 | 86.0 | 12.8 | 128 | 69.6 | 38.0 | 21 | 61.8 | 6.2 |
| | Cw | 75 | 0 | 0.0 | 0.0 | 5 | 2.7 | 6.7 | 1 | 2.9 | 1.3 |
| | Sx | 64 | 5 | 10.0 | 7.8 | 37 | 20.1 | 57.8 | 6 | 17.6 | 9.4 |
| | Bl | 7 | 1 | 2.0 | 14.3 | 5 | 2.7 | 71.4 | 0 | 0.0 | 0.0 |
| | Ep | 3 | 1 | 2.0 | 33.3 | 2 | 1.1 | 66.7 | 2 | 5.9 | 66.7 |
| | Other | 24 | 0 | 0.0 | 0.0 | 7 | 3.8 | 29.2 | 4 | 11.8 | 16.7 |
| Total <i>n</i> | | | 50 | | | 184 | | | 34 | | |
| <i>n</i> | | | 510 | | | 510 | | | 510 | | |
| % | | | 9.8 | | | 36.1 | | | 6.7 | | |
| HL7 | Hw | 310 | 29 | 96.7 | 9.4 | 156 | 83.9 | 50.3 | 23 | 71.9 | 7.4 |
| | Cw | 28 | 0 | 0.0 | 0.0 | 4 | 2.2 | 14.3 | 0 | 0.0 | 0.0 |
| | Sx | 19 | 1 | 3.3 | 5.3 | 17 | 9.1 | 89.5 | 1 | 3.1 | 5.3 |
| | Bl | 13 | 0 | 0.0 | 0.0 | 5 | 2.7 | 38.5 | 5 | 15.6 | 38.5 |
| | Ep | 3 | 0 | 0.0 | 0.0 | 2 | 1.1 | 66.7 | 2 | 6.3 | 66.7 |
| | Other | 6 | 0 | 0.0 | 0.0 | 2 | 1.1 | 33.3 | 1 | 3.1 | 16.7 |
| Total <i>n</i> | | | 30 | | | 186 | | | 32 | | |
| <i>n</i> | | | 379 | | | 379 | | | 379 | | |
| % | | | 7.9 | | | 49.1 | | | 8.4 | | |
| D3 | Hw | 227 | 41 | 87.2 | 18.1 | 158 | 88.3 | 69.6 | 28 | 84.8 | 12.3 |
| | Cw | 18 | 1 | 2.1 | 5.5 | 3 | 1.7 | 16.7 | 1 | 3.0 | 5.5 |

| | | | | | | | | | | | |
|----------------|-------|-----|------|------|------|------|------|-------|------|------|-------|
| | Sx | 1 | 0 | 0.0 | 0.0 | 1 | 0.6 | 100.0 | 0 | 0.0 | 0.0 |
| | Bl/Ba | 29 | 5 | 10.6 | 17.2 | 17 | 9.5 | 58.6 | 3 | 9.1 | 10.3 |
| | Other | 1 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 1 | 3.0 | 100.0 |
| Total <i>n</i> | | | 47 | | | 179 | | | 33 | | |
| <i>n</i> | | | 276 | | | 276 | | | 276 | | |
| % | | | 17.0 | | | 64.9 | | | 12.0 | | |
| PC-M | | | | | | | | | | | |
| C3 | Hw | 83 | 13 | 86.7 | 15.7 | 57 | 69.5 | 68.7 | 15 | 60.0 | 18.1 |
| | Cw | 24 | 0 | 0.0 | 0.0 | 3 | 3.7 | 12.5 | 3 | 12.0 | 12.5 |
| | Sx | 13 | 2 | 13.3 | 15.4 | 8 | 9.8 | 61.5 | 3 | 12.0 | 23.1 |
| | Bl | 15 | 0 | 0.0 | 0.0 | 13 | 15.9 | 86.7 | 3 | 12.0 | 20.0 |
| | Ep | 3 | 0 | 0.0 | 0.0 | 1 | 1.2 | 33.3 | 0 | 0.0 | 0.0 |
| | Other | 2 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 1 | 4.0 | 50.0 |
| Total <i>n</i> | | | 15 | | | 82 | | | 25 | | |
| <i>n</i> | | | 140 | | | 140 | | | 140 | | |
| % | | | 10.7 | | | 58.6 | | | 17.9 | | |
| HL5 | Hw | 104 | 9 | 64.3 | 8.6 | 67 | 75.3 | 64.4 | 10 | 47.6 | 9.6 |
| | Cw | 70 | 0 | 0.0 | 0.0 | 6 | 6.7 | 8.6 | 3 | 14.3 | 4.3 |
| | Sx | 3 | 0 | 0.0 | 0.0 | 2 | 2.2 | 66.7 | 0 | 0.0 | 0.0 |
| | Bl | 11 | 0 | 0.0 | 0.0 | 6 | 6.7 | 54.5 | 2 | 9.5 | 18.2 |
| | Ep | 5 | 2 | 14.3 | 40.0 | 1 | 1.1 | 20.0 | 1 | 4.8 | 20.0 |
| | Other | 27 | 3 | 21.4 | 11.1 | 7 | 7.9 | 25.9 | 5 | 23.8 | 18.5 |
| Total <i>n</i> | | | 14 | | | 89 | | | 21 | | |
| <i>n</i> | | | 220 | | | 220 | | | 220 | | |
| % | | | 6.4 | | | 40.5 | | | 9.5 | | |
| C2 | Hw | 117 | 14 | 87.5 | 12.0 | 57 | 67.9 | 48.7 | 12 | 60.0 | 10.2 |
| | Cw | 56 | 0 | 0.0 | 0.0 | 3 | 3.6 | 5.4 | 2 | 10.0 | 3.6 |
| | Sx | 16 | 1 | 6.3 | 6.2 | 15 | 17.9 | 93.8 | 1 | 5.0 | 6.2 |

| | | | | | | | | | | | |
|----------------|-------|----|------|-------|------|------|------|-------|-----|------|------|
| | Bl/Ba | 7 | 0.0 | 0.0 | 5 | 6.0 | 71.4 | 1 | 5.0 | 5.0 | 14.3 |
| | Ep | 5 | 1 | 6.3 | 20.0 | 3 | 3.6 | 60.0 | 3 | 15.0 | 60.0 |
| | Other | 7 | 0 | 0.0 | 0.0 | 1 | 1.2 | 14.3 | 1 | 5.0 | 14.3 |
| Total <i>n</i> | | | 16 | | | 84 | | | 20 | | |
| <i>n</i> | | | 208 | | | 208 | | | 208 | | |
| % | | | 7.7 | | | 40.4 | | | 9.6 | | |
| PC-O | | | | | | | | | | | |
| D5 | Hw | 98 | 23 | 82.1 | 23.5 | 37 | 74.0 | 37.8 | 8 | 88.9 | 8.2 |
| | Cw | 5 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 |
| | Ba | 17 | 5 | 17.9 | 29.4 | 13 | 26.0 | 76.5 | 1 | 11.1 | 5.9 |
| Total <i>n</i> | | | 28 | | | 50 | | | 9 | | |
| <i>n</i> | | | 120 | | | 120 | | | 120 | | |
| % | | | 23.3 | | | 41.7 | | | 7.5 | | |
| D4 | Hw | 86 | 23 | 100.0 | 26.7 | 56 | 87.5 | 65.1 | 7 | 77.8 | 8.1 |
| | Cw | 14 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0.0 | 1 | 11.1 | 7.1 |
| | Sx | 3 | 0 | 0.0 | 0.0 | 3 | 4.7 | 100.0 | 0 | 0.0 | 0.0 |
| | Ba | 5 | 0 | 0.0 | 0.0 | 5 | 7.8 | 100.0 | 1 | 11.1 | 20.0 |
| Total <i>n</i> | | | 23 | | | 64 | | | 9 | | |
| <i>n</i> | | | 108 | | | 108 | | | 108 | | |
| % | | | 21.3 | | | 59.3 | | | 8.3 | | |

^aThe number of affected trees of each species (*n*).

^bThe percentage of affected trees for each tree species (%-S).

^cThe percentage of all trees of a species that were affected (%-T).

Tree species were: western hemlock (Hw), western redcedar (Cw), hybrid spruce (Sx), subalpine fir (Bl), amabilis fir (Ba), paper birch (Ep). Other species were lodgepole pine (Pl), trembling aspen (At), and black cottonwood (Act).