RESOURCE AVAILABILITY AND LIMITATION FOR A CAVITY-NESTING COMMUNITY IN MATURE CONIFER FORESTS AND ASPEN GROVES IN INTERIOR BRITISH COLUMBIA

by

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ABSTRACT

Nest-site availability limits cavity-nesting populations in harvested forests, and woodpeckers are often considered keystone species because they influence the abundance of other cavity-nesters in the community. However, little is known about the relative importance of excavated versus non-excavated holes for cavity-nesters, and the extent of nest-site limitation in mature forests. I analyzed data from 1371 holes used by 29 bird and mammal species between 1995-2006. Excavated cavities were more abundant than non-excavated and were smaller and higher above ground, but were used in proportion to their availability. To test the hypothesis that nest-site availability limited cavity-nester abundance in mature forests, I conducted two multi-year, replicated before-after/control-impact (BACI) experiments in which I altered nest-site availability. In coniferous forests, which had low cavity densities (1.9/ha) and low occupation rates (9%) prior to treatment, I added nest boxes within the size ranges of the most common excavators (northern flicker *Colaptes auratus* and red-naped sapsucker *Sphyrapicus nuchalis*). Densities of mountain chickadees (*Poecile gambeli*), red squirrels (*Tamiasciurus hudsonicus*), and northern flying squirrels (*Glaucomys sabrinus*) increased following box addition and returned to pre-treatment levels following box removal. In aspen groves, which had high cavity densities (16/ha) and relatively high occupancy rates (44%) prior to my experiment, I blocked the entrances of high quality cavities (those with a high probability of occupancy). Total nest abundance declined by 49% on treatment sites following cavity blocking and returned to pre-treatment levels once cavities were reopened. Nest abundance of European starlings (*Sturnus vulgaris*), a dominant secondary cavity-nester, declined by 89% and failed to recover post-treatment. Conversely, nest abundance of mountain bluebirds (*Sialia currucoides*; a subordinate secondary cavity-nester) increased following cavity blocking and remained high following reopening. While woodpeckers provide an abundant supply of cavities in some mature forests, non-excavated holes may release secondary cavity-nesters from the constraints of excavator

nest-site preferences. Additionally, while nest-sites may appear to be abundant and potentially non-limiting at the community level, individual species preferences, as well as interspecific interactions, may influence true nest-site availability, particularly for mountain chickadees, starlings, and small mammals.

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NOTE: Although I have adopted the convention of using the first-person throughout the thesis, I acknowledge that some of the data used in Chapters 2 and 3 were collected during the long-term “Nest Web” project, directed by my supervisor, Dr. Kathy Martin, UBC. I was personally involved in the data collection from 1997-2005 (as an undergraduate field assistant and project manager from 1997-1999 and as a graduate student from 2000-2005).

DEDICATION

This dissertation is dedicated to my son, Joseph Martin Aitken-Mossop.

CO-AUTHORSHIP STATEMENT

This study was designed collaboratively by Kathryn Aitken and Dr. Kathy Martin. Kathryn Aitken collected the data in the field (1997-2005) with the aid of field assistants, analyzed all data, and prepared the manuscript under the guidance of Dr. Martin.

CHAPTER 1: GENERAL INTRODUCTION AND THESIS OVERVIEW

GENERAL INTRODUCTION

The use of shelters such as tree cavities, burrows and shells for breeding, roosting, and protective cover is common in many animal taxa. One or a few species create these resources, which are then occupied by secondary users that are unable to create their own shelters. For example, soft-bodied hermit crabs (Anomura: Superfamily Paguroidea) require empty gastropod shells for protection from predators (Hazlett 1981). Several bird species including golden-shouldered parrots (*Psephotus* spp.), parakeets (*Brotogeris* spp.), trogons (*Trogon* spp.), and kingfishers (*Todiramphus* spp.), as well as caimans (*Paleosuchus* spp.), African giant rats (*Cricetomys gambianus*), and eumenid wasps (Hymenoptera: Eumenidae) raise their offspring in or on termitaria, which provide heat and cover (Ajayi 1977, Batra 1979, Weaver 1982, Magnusson et al. 1985, Brightsmith 2000, Kesler and Haig 2005). Prairie dog (*Cynomys* spp.) burrows provide shelter and nest sites for burrowing owls (*Athene cunicularia*) and for other birds, mammals, reptiles, and amphibians (Clark et al. 1982, Desmond and Savidge 1996). However, availability of shelters is limited for many of these secondary users (Vance 1972, Abrams et al. 1986, Newman 1987, Lindenmayer et al. 1991, Newton 1994, McCallum et al. 2001), and the costs and benefits of acquiring or defending critical but limited shelters provided by other species results in hierarchical nidic structure, or "nest webs", analogous to trophic structure in food webs (Martin and Eadie 1999).

Species that rely on tree cavities form one of the largest groups of shelter users. These species, which include birds, mammals, reptiles, amphibians, and insects, use holes in trees for nesting, roosting, food storage, and cover. Approximately 85 bird and 20 mammal species in Canada and the continental United States use tree cavities (Burt and Grossendeider 1980, Ehrlich et al. 1988, Martin and Scotton unpubl. data), and five percent of European bird species are obligate hole-nesters (Newton 1994). Cavity-nesting communities are structured hierarchically in a nest web of interdependencies based on nesting, foraging and other interactions (Martin and Eadie 1999, Martin et al. 2004). Woodpeckers, or primary cavity excavators, create holes for nesting and roosting. Some woodpeckers use old cavities but little is known about the costs and benefits of reuse for these excavator species (Wiebe et al. 2007). Cavities created by woodpeckers are used by secondary cavity nesters, a diverse group, including passerines such as bluebirds (*Sialia* spp.) and some swallows (*Tachycineta* spp.), several species of ducks and raptors, and some small mammals. Because secondary cavity-nesters cannot excavate their own nest holes, they are dependent on those provided by woodpeckers, or on naturally occurring holes caused by tree decay or damage. Weak cavity excavators, including nuthatches (*Sitta* spp.) and some chickadees (*Poecile* spp.), may excavate a cavity on their own, enlarge a hole begun by a woodpecker, or use a naturally occurring non-excavated hole (Aitken et al. 2002).

The importance of excavated versus non-excavated holes for cavity-nesters

Woodpeckers are considered keystone species in some forest communities and can influence the diversity and abundance of other members of the community (Van Balen et al. 1982, Daily et al. 1993, Mikuskinski and Angelstam 1998, Martin and Eadie 1999, Aubry and Raley 2002, Duncan 2003). For example, woodpeckers may act as physical ecosystem engineers by excavating nesting and roosting cavities that are used by other cavity-nesting species in the community, by creating foraging opportunities for other species through excavation of feeding holes, sapwells, and bark-scaling, and by accelerating tree decay processes and heartrot inoculation (Ehrlich and Eaily 1988, Jones et al. 1994, 1997, Aubry and Raley 2002, Duncan 2003, Conner et al. 2004, Martin et al. 2004). Woodpeckers may also serve as indicators of species richness and abundance in forest communities, and of overall forest health (Angelstam and Mikusinski 1994, Mikusinski et al. 2001, Remm et al. 2006).

In addition to woodpecker-excavated cavities, naturally-occurring non-excavated holes provide nest and roost sites for cavity-nesting species. These holes develop through a variety of mechanisms, including tree limb or top breakage, loosening of bark, wound openings, and a range of fungal and disease processes. However, little is known about the relative abundance and importance of excavated versus non-excavated holes for cavity-nesters in undisturbed forest ecosystems (Martin and Wesolowski, in review). The value of excavators as cavity providers may depend on the abundance of naturally occurring non-excavated holes (Carlson et al. 1998, Remm et al. 2006, Wesolowski in review). Non-excavated holes may free secondary cavity-nesters from the constraints of woodpecker nest-site characteristics and habitat selection, and offer excavator species alternate nesting options if time or energy for excavation is limited. However, if non-excavated cavities are scarce in the landscape then it may be difficult for secondary users to locate holes with suitable characteristics or in optimal habitat. In that case, excavated holes may provide the most options for secondary users, particularly if the woodpecker assemblage in the community is diverse.

The role of nest-site availability in limiting cavity-nesting populations

Because cavity-nesters depend on trees for nesting and other activities, they are considered sensitive to forest harvesting (Angelstam and Mikusinski 1994, Newton 1994) and the presence of suitable nest-sites limits some populations of obligate cavity-nesters (Scott 1979, Newton 1994, Bock and Fleck 1995). This is especially true for secondary cavity-nesting species, which cannot excavate their own cavities. Weak excavators, which require soft decaying substrate, may be limited by the availability of dead or dying trees (Steeger and Hitchcock 1998). These trees may be rare in some forests because they are susceptible to wind throw and are often removed or knocked down during logging operations (Thomas et al. 1979, De Long et al. 2004). In interior British Columbia, more than 90% of cavity nests were located in dying or dead trembling aspen, which made up only 10-15% of trees in the landscape (Martin and Eadie 1999, Martin et al. 2004). However, most studies of nest-site limitation in cavity-nesters have been conducted in managed forests in which the natural assemblage of excavator species may have been altered, and in which essential habitat features such as standing dead and unhealthy trees have been removed (Newton 1994). The few studies conducted in mature forests in which natural rates of cavity creation and loss have not been altered suggest that predation and food availability may be the main factors limiting cavity-nesting populations in those systems (Wesolowski 1989).

Species in communities structured around a central resource such as tree cavities may adopt a variety of strategies to acquire that resource. Plasticity in resource selection may allow individuals to reduce interspecific competition and to adapt to temporal and spatial changes in resource availability (Albano 1992, Cuervo 2004, Forstmeier and Weiss 2004, Eggers et al. 2006). Generalist species may be better able to withstand stochasticity in resource availability than specialists (Pimm and Pimm 1982, Palmer 2003), while specialists may put more effort into acquiring a limited number of higher quality resources. Species in cavity-nesting communities display a range of resource acquisition and competitive strategies, thus providing an excellent system in which to examine the importance of ecological plasticity in community responses to changes in resource availability and quality.

Nest-site availability and limitation in mature forests of interior British Columbia

The Cariboo-Chilcotin region of interior British Columbia consists of mature mixed conifer forests, and native grassland interspersed with small groves of trembling aspen (*Populus tremuloides*). There are 42 species of cavity-using birds and small mammals in the region, including 8 of 12 woodpecker species found in the province (Martin et al. 2004), and almost one-quarter of the bird species in the region are cavity-nesters. Cavity density ranges from low

(1.9/ha) in coniferous forests to high (16/ha) in aspen groves, and occupancy rates vary from 9% in coniferous forests to 44% in aspen groves (Aitken 2002, Aitken and Martin 2004). I found a positive relationship between nest density and cavity density (curve estimation procedure, SPSS Inc. 2002; aspen groves: 2000, quadratic model, $R^2 = 0.69$, $F_{2, 28} = 31.3$, $P < 0.0001$, 2001, linear model, $R^2 = 0.47$, $F_{1, 29} = 25.4$, $P < 0.0001$, Figure 1.1a; coniferous forests: 2000: linear model, $R^2 = 0.06$, $F_{1, 5} = 0.30$, $P = 0.61$, 2001: linear model, $R^2 = 0.004$, $F_{1, 5} = 0.02$, $P = 0.89$, Figure 1.1b), which may indicate nest-site limitation (Raphael and White 1984, Newton 1994). Cavity density was a significant predictor of nest density in both aspen groves and coniferous forests in the study area (linear mixed-effects model; Table 1.1).

THESIS OBJECTIVES

My study addressed the general question of how plasticity in nest-site selection enables species and communities to respond to fluctuations in abundance and quality of a critical resource (nesting cavities). My objectives were to examine the importance of excavated versus non-excavated holes for cavity-nesting birds and mammals (Chapter 2), and to determine whether cavity abundance limits cavity-nester populations in mature mixed conifer forests (Chapter 3) and aspen groves (Chapter 4).

STUDY AREA

Fieldwork was conducted in mature coniferous forests (80-200 yr old) and aspen groves on Becher's Prairie, near the community of Riske Creek (51° 52'N, 122°21'W, 850-1000m elevation; Figure 1.2). Coniferous forests (>100 ha) were dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), with varying amounts of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), hybrid white-Engelmann spruce (*Picea glauca* x *engelmanni*), and aspen (Martin et al. 2004). These forests bordered on grassland or lakes. Aspen groves ranged in size from just a few trees to several hectares, and were scattered throughout the grassland matrix. Some were surrounded by grassland while others bordered on ponds or marshes. Table 1.2 presents a summary of the 28 cavity-nesting bird and mammal species nesting on my study sites between 1995-2006, and indicates their primary nesting habitat (coniferous forest or aspen groves), based on the proportion of nests found in each habitat type. See individual data chapters for details of specific study sites and methodology.

THESIS OVERVIEW

In Chapter 2, I examined the relative availability and use of excavated and non-excavated cavities in aspen groves and coniferous forest between 1995-2006. I compared cavity, tree and habitat characteristics of excavated and non-excavated holes used for nesting at the community-level, and for five individual species (northern flicker *Colaptes auratus*, mountain chickadee *Poecile gambeli*, mountain bluebird *Sialia currucoides*, tree swallow *Tachycineta bicolor*, and European starling *Sturnus vulgaris*). I found that, while excavated cavities were much more abundant than non-excavated cavities and species from all three guilds used non-excavated holes, most species appeared to use them in proportion to their availability. I then reviewed the findings of the few previous studies that examined excavated versus non-excavated holes for cavity-nesters, and discussed the possible advantages for secondary cavity-nesters and excavators that use non-excavated holes.

In Chapter 3, I examined nest-site limitation in mature coniferous forests with low cavity densities and occupation rates, using a box addition experiment. I compared nest densities for all cavity-nesting species combined, as well as for several individual species (mountain chickadee, red-breasted nuthatch, red squirrel, and northern flying squirrel) on treatment (box addition) and control sites over an 11-year period (six years pre-treatment, two years during treatment, and three years following box removal). I found that nest densities of mountain chickadees and nuthatches, and nest and roost densities of squirrels increased significantly following the experimental increase in nest-site availability, and returned to pre-treatment levels when boxes were removed. I then reviewed recent studies examining limitation of cavity-nester populations in mature forests, and interpreted my results in light of chickadee, nuthatch, and squirrel social behaviour and life history strategies.

In Chapter 4, I examined the potential for nest-site limitation in aspen groves with high cavity densities by blocking the entrances of high quality cavities (those with past high occupancy rates). Using generalized linear mixed-effects models, I compared nest abundance of all cavity-nesting species combined, as well as for several individual species (European starlings, mountain bluebirds and tree swallows) on treatment and control sites for two years prior to treatment, two years during treatment, and two years following cavity reopening. I found that species with generalist nest cavity preferences displayed high resistance in nest abundance following the experimental decrease in nest-site availability, while the most dominant, specialist cavity-nester, European starling, displayed low resistance and resilience to cavity blocking. I also found that mountain bluebirds, a subordinate secondary cavity-nester, appeared to be limited by starling nest abundance. I discuss the implications of generalist versus specialist resource acquisition strategies in determining the response to perturbation, as well as dominance and competitive ability, for cavity-nesters using temporally or spatially variable resources.

In chapter 5, I summarized the conclusions of my research chapters. I also provided a summary of knowledge gaps in cavity-nester community and population ecology, and suggested directions for future research that could address these questions.

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

Table 1.1. Linear mixed-effects model predicting nest density of cavity-nesting birds and mammals in mature coniferous forests and aspen groves in interior British Columbia, Canada in 2000 and 2001, in relation to cavity density. Year was included in the model as a random effect. Data were log-transformed for analysis.

Parameter	**Estimate**	**SE**	**df**	***t*-statistic**	***P***
Intercept	-0.78	0.19	72	-4.2	0.0001
Log cavity density	1.78	0.24	72	7.5	<0.0001
Site type (conifer forest or aspen grove)	-0.60	0.33	72	-1.82	0.07

Table 1.2. Cavity-nesting bird and mammal species found in aspen groves and coniferous forests near Riske Creek, British Columbia, 1995-2006. Primary nesting habitat is indicated as “Coniferous” or “Aspen groves” when >60% of a species’ nests were located in those forest types; “Both” indicates that ~50% of a species’ nests occurred in each habitat. For species with n < 5, the predominant nesting habitat is shown in brackets. Total sample size of nests is n = 2262 for the study.

Species	**Code**	**Nesting habitat**	**Total nests**
Primary cavity excavators			
Red-naped sapsucker (*Sphyrapicus nuchalis)*	RNSA	Both	214
Downy woodpecker (*Picoides pubescens)*	DOWO	Coniferous	24
Hairy woodpecker (*Picoides villosus)*	HAWO	Coniferous	36
American three-toed woodpecker (*Picoides dorsalis)*	ATTW	Coniferous	6
Black-backed woodpecker (*Picoides arcticus*)	BBWO	(Coniferous)	2
Northern flicker (*Colaptes auratus)*	NOFL	Aspen groves	348
Pileated woodpecker (*Dryocopus pileatus*)	PIWO	Coniferous	17
Weak cavity excavators			
Black-capped chickadee (*Poecile atricapillus)*	BCCH	Both	35
Red-breasted nuthatch (*Sitta canadensis)*	RBNU	Coniferous	154
Secondary cavity nesters			
Wood duck (*Aix sponsa*)	WODU	(Aspen groves)	1
Bufflehead (*Bucephala albeola)*	BUFF	Aspen groves	59
Barrow’s goldeneye (*Bucephala islandica*)	BAGO	Aspen groves	5
Hooded merganser (*Lophodytes cucullatus*)	HOME	(Aspen groves)	2
American Kestrel (*Falco sparverius)*	AMKE	Aspen groves	40
Flammulated owl (*Otus flammeolus*)	FLOW	(Aspen groves)	1
Northern saw-whet owl (*Aegolius acadicus*)	NSWO	Aspen groves	18
Northern hawk owl (*Surnia ulula*)	NHOW	(Aspen groves)	2
Tree swallow (*Tachycineta bicolor)*	TRES	Aspen groves	257
Mountain chickadee (*Poecile gambeli)*	MOCH	Both	333
Mountain bluebird (*Sialia currucoides)*	MOBL	Aspen groves	266
European starling (*Sturnus vulgaris)*	EUST	Aspen groves	340
Northern flying squirrel (*Glaucomys sabrinus*)	GLSA	Coniferous	17
Bushy-tailed woodrat (*Neotoma cinerea)*	NECI	Aspen groves	7
Red squirrel (*Tamiasciurus hudsonicus)*	TAHU	Both	73
Chipmunk spp. (*Eutamias* spp.)		(Coniferous)	2
Short-tailed weasel (*Mustela erminea*)	MUER	(Aspen groves)	1
Fisher (*Martes pennanti*)	MAPE	(Coniferous)	1
Deer mouse (*Peromyscus maniculatus*)	PEMA	(Aspen groves)	1

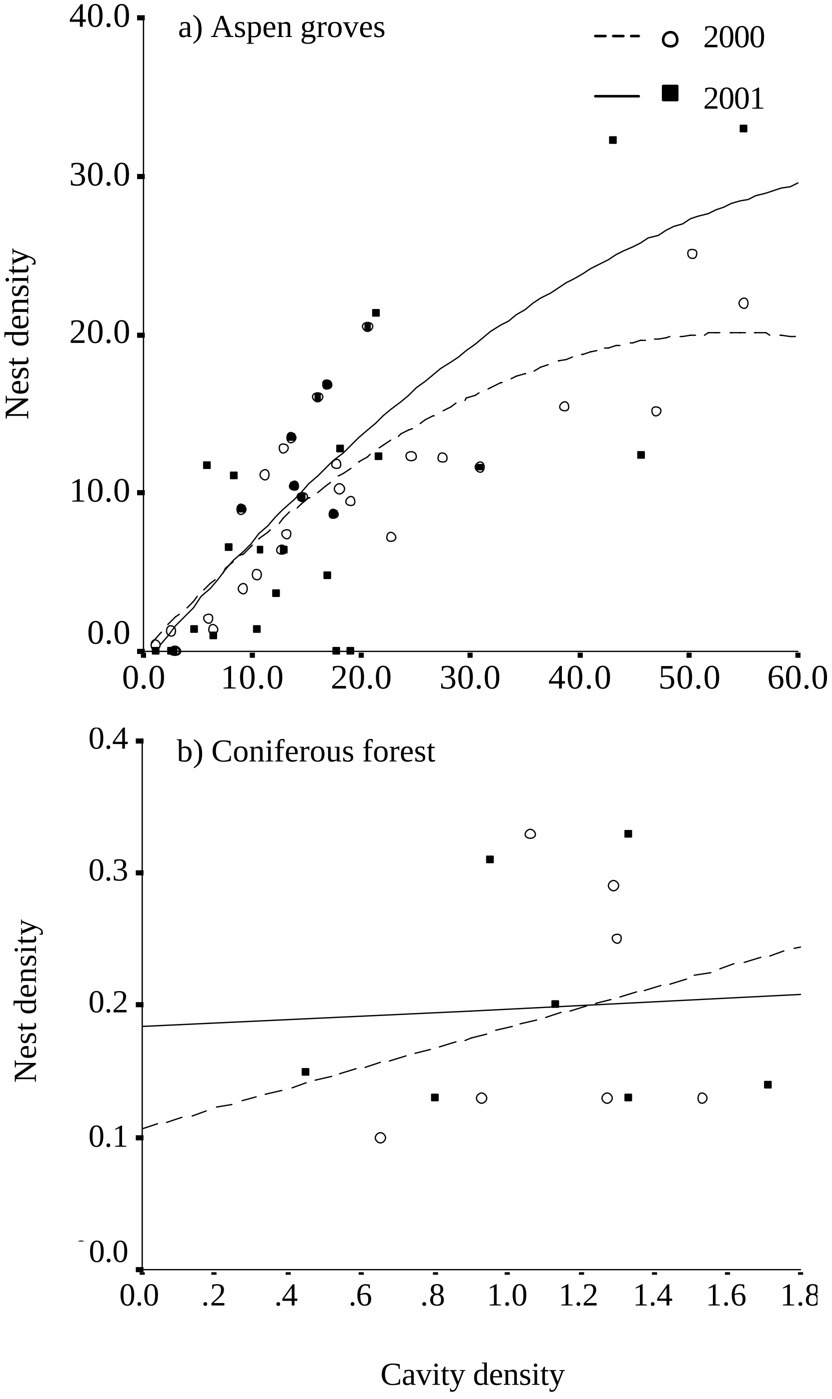

Figure 1.1. Relationship between density of cavity-nesting birds and mammals and total cavity density in a) aspen groves and b) mature coniferous forest in interior British Columbia in 2000 and 2001. See text for results of statistical tests.

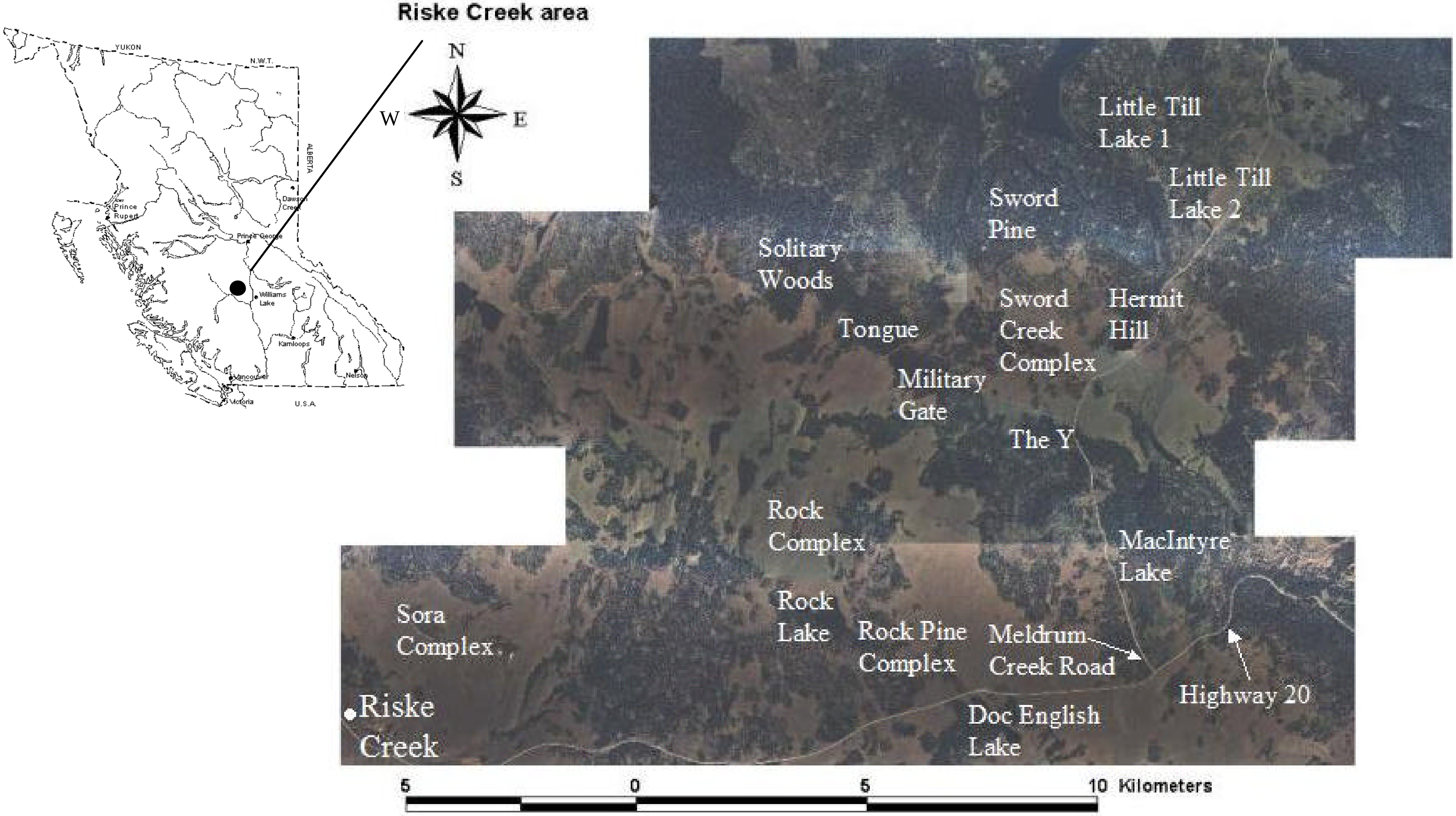

Figure 1.2. Map of British Columbia indicating the location of the study area near Williams Lake, and aerial photograph of the study area with study sites labelled.

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CHAPTER 2: THE IMPORTANCE OF EXCAVATORS IN CAVITY-NESTING COMMUNITIES: AVAILABILITY AND USE OF NATURAL TREE CAVITIES IN OLD MIXED FORESTS OF WESTERN CANADA.[1]

INTRODUCTION

A broad range of bird, mammal, reptile, amphibian, and insect species worldwide use cavities in trees for nesting, roosting, food storage, and cover, including over 100 bird and mammal species in North America (Burt and Grossenheider 1980, Newton 1998). Tree cavities provide secure sites from predators and inclement weather, and their availability and distribution are considered to shape life history traits and community structure for the group (Martin 1993, Martin et al. 2004, Wiebe et al. 2006). Excavators such as woodpeckers create cavities in dying or dead wood. Non-excavated cavities may originate from broken tree limbs, crevices behind bark, hollow stumps, wound openings and a range of fungal and other decay processes. Cavities may remain in the landscape for several years to decades, providing a required nesting resource for non-excavating secondary cavity-nesters, and an option for excavators to reuse existing cavities (Aitken et al. 2002, Wiebe et al. 2006).

Woodpeckers are considered to be keystone species in many systems because, by providing nest-sites for secondary cavity-nesters, they may influence the abundance and distribution of other species in the community (Daily et al. 1993, Martin and Eadie 1999). However, in some systems non-excavated cavities may be plentiful enough that excavated cavities are used relatively infrequently or are avoided by secondary cavity-nesters (Carlson et al. 1998, Remm et al. 2006, Wesolowski, in review). Non-excavated cavities may also be less susceptible to predation by large woodpecker species than excavated cavities (Walankiewicz

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2002, Wesolowski 2002). However, few studies have examined differences between excavated and non-excavated cavities. In many studies of nest-site selection, cavity origin is not recorded. Comparing use and availability of excavated and non-excavated cavities may provide insight into the importance of woodpeckers as keystone species, and into the nest-site requirements of secondary cavity-nesters when they are released from the constraints of woodpecker nest-site preferences and, potentially, competition for excavated cavities.

The cavity-nesting bird and mammal community of Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests of central British Columbia, Canada is one of the richest in North America (Martin and Eadie 1999). Approximately 22% of the bird species in the region are cavity-nesters and both excavators and non-excavators use non-excavated cavities (Martin and Eadie 1999, Aitken and Martin 2004). In this paper, I examine use of excavated and non-excavated cavities by excavators and secondary cavity-nesters, and compare characteristics of excavated and non-excavated cavities used for nesting at the community level, and by several individual species. I also consider cavity type in relation to forest context, and present the results of a survey of availability of excavated and non-excavated cavities.

METHODS

Study Area

Nest cavities were located and monitored on a total of 15 study sites at Riske Creek between 1995-2006, eleven of which were mature coniferous forest (Doc English Lake, Hermit Hill, Little Till Lake 1, Little Till Lake 2, MacIntyre Lake, Military Gate, Rock Lake, Solitary Woods, Sword Pine, Tongue, The Y; Figure 1.2), and four of which were complexes of aspen groves (Rock Complex, Rock Pine, Sora Complex, Sword Creek). An additional 12 coniferous forest study sites were monitored near 150 Mile House, BC, approximately 60 km southeast of Riske Creek.

Nest location and monitoring

From 1 May to 31 July 1995-2006, all sites were searched for occupied cavity nests. In my study area, most migratory and resident cavity nesters did not begin nesting until the first or second week of May. Systematic nest searches were conducted across all sites for an average of 6-7 observer-hours of nest searching per sampling site per week. Because cavity nesters reused cavities and nest trees in multiple years (Aitken et al. 2002), existing cavities were checked (both previously used and those not known to be occupied in previous years), as well as newly excavated cavities.

Occupied cavities were located by looking or listening for excavation, by tapping or scraping at the base of trees containing cavities to detect occupants, and by observing breeding birds or hearing begging nestlings. Finding occupied nests was facilitated by detecting general locations of cavity nesters during early morning point-count surveys. Cavities within reach of a ladder (≤ 5.2m) were inspected visually with flashlights and mirrors. In 2005 and 2006, a TreeTop Peeper™ camera system (Sandpiper Technologies, Manteca, CA, USA) was used to monitor cavities up to 17 m, and in trees too unstable to reach with a ladder. Nests were considered occupied if they contained at least one egg or nestling. I also monitored cavities occupied by cavity-nesting mammals such as red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), and bushy-tailed woodrat (*Neotoma cinerea*), as well as use by facultative cavity users such as deer mouse (*Peromyscus maniculatus*), short-tailed weasel (*Mustela erminea*), fisher (*Martes pennanti*), and chipmunk (*Eutamias* spp.). Occupied cavities were assigned unique numbers and nest trees were marked with numbered aluminum tags to facilitate relocation across the study years.

Nest tree and cavity characteristics

After nest cavities were vacated, I recorded tree and cavity variables. Cavity origin was categorized as excavated or non-excavated. Because non-excavated cavities were located in broken branch nodes, behind bark, tops of stumps, etc., these were clearly distinguishable from excavated holes. The species of the cavity excavator was recorded if observed during excavation, or occasionally from diagnostic features such as entrance size and shape. Tree characteristics included species, decay stage (live or dead), and diameter at breast height (DBH). Cavity variables included height above ground (m), vertical depth (cm), internal diameter (cm), entrance height and width (cm), and orientation. Vertical depth was measured from the bottom of the cavity entrance to the floor of the cavity. Internal diameter was measured from the inner edge of the lower lip of the entrance to the back wall of the cavity. Entrance area (cm^2) was calculated using entrance height and width and the formula for the area of an ellipse. Distance to nearest forest edge (grassland, pond, or stream) was recorded either directly using 30 m measuring tapes or by global positioning system (GPS).

Availability of excavated and non-excavated cavities

In 2000, I surveyed cavity availability in 5 coniferous forest sites, and in 35 aspen groves (0.05 – 3 ha). At each coniferous forest site, I established 3 transect lines, 100 m apart, starting at the forest edge and extending 350 m into the forest. Walking along each transect, I recorded all cavities within 10 m on either side of the line. In each aspen grove, I searched throughout the entire patch, recording all cavities. The same two observers surveyed each site to ensure that cavity-searching techniques were consistent among sites. I did not include partially excavated trial cavities in my surveys, or cavities with a vertical depth of <1 cm. I recorded tree and cavity characteristics as described above for nest cavities.

Data analyses

I used linear mixed effects (LME) models to determine whether tree and cavity characteristics differed among nests in excavated and non-excavated cavities. Nest-site variables examined were height above ground, vertical depth, internal diameter, entrance area, tree DBH, and distance from grove or forest edge. Data were analyzed using the procedure LME in the statistical program R (R version 2.4.0, R Development Core Team 2006). I built separate models for each nest-site variable. Each model included the dependent variable of interest (e.g. height above ground) and cavity type (excavated or non-excavated) as the fixed effect. Because cavities were used multiple times across years, I included individual cavity as a random effect in each model. Distance to edge followed a Poisson distribution in coniferous forest sites; thus, I used generalized linear mixed models with a penalized quasi-likelihood method of parameter estimation (glmmPQL; Breslow and Clayton 1993, Nelson and Leroux 2006) to compare distance to edge among excavated and non-excavated cavities in those sites. PQL is an approximate method of inference in GLMMs in which maximum likelihood methods are not appropriate due to the distribution of random effects (Wedderburn 1974, Breslow 2003). Independent samples *t*-tests were used to compare characteristics of excavated and non-excavated cavities recorded in my 2000 cavity availability survey. Where necessary, data were log- or square-root transformed in order to meet assumptions of normality and equality of variance. Where data could not be transformed to meet assumptions, non-parametric Mann-Whitney *U*-tests were used. I tested whether orientation of excavated and non-excavated cavity entrances was random or non-random using one-sample Watson's U^2 tests for circular distributions, and mean orientation of excavated and non-excavated cavities were compared using two-sample Watson's U^2 test in the statistical program Oriana (Oriana version 2.0.2, Kovach Computing Services 2005). Chi-square tests were used to compare proportions of excavated and non-excavated cavities in coniferous forests versus aspen groves, and in live versus dead trees.

RESULTS

Excavated versus non-excavated cavities used for nesting

I was able to identify mode of creation (excavated or non-excavated) for 1371 individual cavities used for nesting in 1057 trees on my study sites between 1995-2006. Ninety-five percent of these cavities were excavated and 5% were non-excavated. Red-naped sapsucker (*Sphyrapicus nuchalis*) and northern flicker excavated 52% of all cavities, 19% were excavated by other woodpecker species, and 11% were excavated by chickadees or red-breasted nuthatch (*Sitta canadensis*; Table 2.1). Among non-excavated cavities, most were in broken branch nodes, crevices behind loose bark, and hollow stumps ("chimneys"). Two unusual mountain bluebird nests (one wedged in a cracked boulder, the other in the hollow end of a metal bridge piece) were not included in my analyses of non-excavated cavities.

I monitored 2728 nesting attempts, 94% of which were in excavated cavities, and 6% in non-excavated cavities. As expected, the proportion of nests in non-excavated cavities differed among excavators and secondary cavity-nesters, with 10% of secondary cavity-nester nests in non-excavated cavities, and just 2% of excavator nests in non-excavated cavities. While northern flicker was the only woodpecker that used both excavated and non-excavated cavities, only 4% of flicker nests were in non-excavated holes (Table 2.1). The only species that used non-excavated cavities more than 20% of the time was the bushy-tailed woodrat (*Neotoma cinerea*; Table 2.1).

With all species grouped together, nests in excavated cavities were on average almost two meters higher above ground than nests in non-excavated cavities (Figure 2.1a, Table 2.2). Excavated cavities used for nesting were significantly narrower internally (Figure 2.1c), and had smaller entrances than non-excavated cavities (Figure 2.1d, Table 2.2). Vertical cavity depth and tree diameter at breast height did not differ among excavated and non-excavated cavities used for nesting when all species were grouped (Figures 2.1b and e, Table 2.2). While there was little difference in distance to nearest edge among nests in excavated and non-excavated cavities in aspen groves, nests in excavated cavities in coniferous forest were farther from edge than were those in non-excavated cavities (Figure 2.2). However, this was not significant in my mixed model analysis (Table 2.2). Orientations of excavated and non-excavated cavities were non-random, with more cavities facing southwest than other directions (Watson's one-sample U^2 test; excavated cavities: $\mu = 211° \pm 100°$, $U^2 = 3.1$, N = 1289, $P < 0.005$; non-excavated cavities: $\mu = 203° \pm 99°$, $U^2 = 0.2$, N = 64, $P < 0.05$; Figure 2.3). Mean orientation did not differ between excavated and non-excavated cavities (Watson's two-sample U^2 test: $U^2 = 0.07$, $P > 0.05$, N = 1289, 64).

Five species had large enough sample sizes to allow me to compare characteristics of nests in excavated and non-excavated cavities: northern flicker, mountain chickadee, mountain bluebird, European starling, and tree swallow. Northern flicker nests in excavated cavities were significantly higher above ground and shallower than non-excavated cavities (Figure 2.1, Table 2.2). Mountain chickadee nests in excavated cavities were significantly shallower than non-excavated cavities (Figure 2.1, Table 2.2). In coniferous forests, mountain chickadee nests in excavated cavities were significantly farther from edge than were nests in non-excavated cavities (Figure 2.2, Table 2.2). This trend was reversed in aspen groves, where mountain chickadee nests in non-excavated cavities were more than twice as far from edge as were excavated cavities (Figure 2.2, Table 2.2). Of the five species examined, only mountain chickadees nested in both excavated and non-excavated cavities in coniferous forest sites (Figure 2.2). Mountain bluebird nests in excavated cavities were significantly higher above ground, had considerably smaller entrances, and were in smaller trees than were non-excavated cavities (Figure 2.1, Table 2.2).

There were few differences between excavated and non-excavated cavities used by European starling, although entrance areas of excavated starling nests were significantly larger than those of non-excavated cavities (Figure 2.1, Table 2.2). Tree swallow nests in excavated cavities were significantly higher above ground, narrower internally and had smaller entrances than did nests in non-excavated cavities (Figure 2.1, Table 2.2).

Availability of excavated versus non-excavated cavities

In 2000, I surveyed 200 available cavities, of which 85% were excavated and 15% were non-excavated. Mean density of excavated cavities was 11.2 per hectare, versus 1.1 per hectare for non-excavated cavities. Aspen groves had a slightly lower proportion of non-excavated cavities than coniferous forests (14% of 180 cavities in aspen groves, 20% of 20 cavities in coniferous) but this difference was not significant ($X^2 = 0.44$, df = 1, N = 200, $P = 0.5$). While non-excavated cavities were similar to excavated cavities in height above ground, internal diameter and distance to nearest edge, they tended to be deeper and have larger entrances, but not significantly so (Table 2.3). Trees with excavated cavities did not differ in stage of decay from those with non-excavated cavities (Live versus dead: $X^2 = 0.02$, df = 1, N = 200, $P = 0.9$).

DISCUSSION

Both the availability and use of excavated and non-excavated cavities varies across forest types and ages, landscape types, and possibly across continents (Wesolowski, in review). Costs and benefits associated with cavity origin, and competitive abilities to secure a preferred cavity type, may vary among species. Here, I discuss the variation in abundance and use of the two major cavity types across species and in relation to forest type and context for northwestern North America.

Previous studies in forests of Europe and Asia reported a wide range in the relative abundance of excavated and non-excavated cavities. Remm et al. (2006) found that woodpeckers excavated 88% of cavities in deciduous forests in Estonia, while Carlson et al. (1998) found that 47% of cavities in Swedish deciduous forest were excavated. In contrast, in old-growth mixed forests in eastern Poland, non-excavated cavities were much more abundant than excavated cavities (11-11.5 *vs* 4.5-5 cavities/ha) and about 90% of secondary cavity-nesters nested in non-excavated cavities (Wesolowski, in review). In Mongolian mature forests, 75% of nesting attempts were in non-excavated cavities (Bai et al. 2003). On my study sites, excavated cavities were much more abundant (11.2 cavities/ha) than non-excavated cavities (1.1/ha). Woodpeckers were abundant in my region and individuals may excavate multiple cavities each year (Bonar 2000, Walters et al. 2002). Because these cavities are often excavated in live trees or those in the earliest stages of decay, these cavities may persist for several years to over 30 years (Aitken et al. 2002, Wesolowski, in review). If excavated cavities are created at a faster rate than non-excavated cavities or survive longer, this may lead to a greater supply of excavated cavities compared to non-excavated cavities in the landscape.

While secondary cavity-nesters as a group used excavated and non-excavated cavities approximately in proportion to their availability in the landscape, use of non-excavated cavities varied among species. The larger secondary cavity-nester species, bufflehead (*Bucephala albeola*), Barrow’s goldeneye (*Bucephala islandica*), American kestrel (*Falco sparverius*), and northern saw-whet owl (*Aegolius acadicus*) used non-excavated cavities less frequently than some of the smaller secondary cavity-nesters, such as bluebird and starling. Although non-excavated cavities tended to be larger on average than excavated cavities, these cavities were also relatively scarce. Therefore, large-bodied cavity-nesters may be constrained by the availability of large cavities and rely primarily on those created by large excavators (Martin et al. 2004).

There were ten excavating species in my study region, including 10-11 g chickadee and nuthatch, and eight species of woodpecker ranging in mass from the 30 g downy woodpecker (*Picoides pubescens*), to the 300 g pileated woodpecker (*Dryocopus pileatus*; Campbell et al. 1990, Bull and Jackson 1995, Martin and Norris 2007). This excavator group provides cavities across a broad range of habitat types that accommodate an array of secondary cavity-nesters from 10 g chickadees to 1 kg Barrow's goldeneye and 2.5 kg fisher (Martin et al. 2006). In European forests, woodpecker species diversity was positively correlated with secondary cavity-nester diversity, likely due to an increase in cavity diversity in stands with a variety of woodpeckers (Mikusinski and Angelstam 1998). With a broad range of excavating species in the community and, thus, a wide variety of potential nest-sites available, secondary cavity-nesters may not be as dependent on non-excavated cavities as in systems in which the excavator assemblage has been altered.

Three excavators, northern flicker, red-breasted nuthatch, and black-capped chickadee (*Poecile atricapillus*) used a small proportion of non-excavated cavities for nesting in my sites. Nuthatches and chickadees are weak excavators that require trees in advanced stages of decay for excavation, and may be limited by the availability of these trees (Dickson et al. 1983, Steeger and Hitchcock 1998). Naturally occurring cavities may provide ready-made nest-sites when suitable trees are unavailable for excavation for these species. The only woodpecker to use non-excavated cavities in my study, northern flicker, experiences aggressive competition from European starlings, and is often evicted from its nest cavities (Moore 1995, Wiebe 2003). Use of non-excavated cavities may be a means to avoid competition from starlings and other secondary cavity-nesters, and may allow excavators to initiate breeding earlier (Wiebe et al. 2006).

Non-excavated cavities used for nesting tended to be larger internally and had larger entrances than excavated cavities. Both cavity entrance size and internal size have been linked with fecundity and reproductive success in cavity-nesters. Cavities with larger volume may allow for larger clutch sizes, better thermoregulation by nestlings, or better protection from predators (Alatalo et al. 1988, Slagsvold 1989, Wiebe and Swift 2001). Conversely, cavities with small entrances may restrict access by medium and large nest predators (Wesolowski 2002). Among species using non-excavated cavities, there may be a trade-off between the potential advantage of larger internal area and the potential disadvantage of larger entrance area. However, among species that use non-excavated cavities somewhat regularly (e.g., starlings, bluebirds), clutch size, hatch success and fledge success in non-excavated cavities all increased with increasing frequency of use of non-excavated cavities (Martin, unpublished data). For these species, the potential advantages of non-excavated cavities, such as reduced competition for nest-sites, and increased cavity volume, may outweigh any disadvantages.

Of the five species examined in-depth, starlings selected excavated and non-excavated cavities for nesting that were the most similar to each other. Although starlings are considered to be nest-site generalists because they have adapted successfully to nesting in both natural and human-made structures, nest-site selection studies of starlings suggest that they are actually quite specialized in their nest-site preferences. In a nest-site selection study of cavity-nesters in Poland, starlings had stronger preferences for cavities based on tree species, height above ground, and cavity entrance shape than most other species in the community (Wesolowski 1989). Starlings in the Netherlands and Sweden preferred cavities that were large internally (van Balen et al. 1982, Carlson et al. 1998). In an earlier study, I found that starlings preferred nest-sites that were larger internally, closer to grassland edge, and in trees with only one cavity (Aitken and Martin 2004). In urban areas of Ontario, Canada, starlings used a smaller range of human-made structures for nesting and with a narrower range in characteristics than another introduced secondary cavity-nester, the house sparrow (*Passer domesticus*; Savard and Falls 1981). These strong nest site preferences may cause starling populations to be limited by the availability of suitable cavities. In an experiment in which I blocked the entrances of preferred nest cavities, the number of starling nests declined significantly and did not recover following reopening of cavities (Chapter 4). Starlings are successful competitors for nest-sites, either through direct interference with other cavity-nesters or indirectly through timing of breeding (Ingold 1994, 1996, Wiebe 2003, Fisher and Wiebe 2006), and thus may be better able to acquire higher quality non-excavated cavities than other less competitive or later nesting species.

I observed an abundant supply of natural (excavated and non-excavated) cavities on my predominantly mature sites in British Columbia (12.3 cavities/ha), as did Wesolowski (in review) in old-growth temperate forest in eastern Poland (16 cavities/ha). Interestingly, in both studies, secondary cavity-nesters primarily used the more abundant cavity type (excavated holes in my study sites, non-excavated holes in Wesolowski’s sites). In both studies, it appeared that cavity supply exceeded demand, with the majority of cavities unoccupied each year (Aitken et al. 2002, Aitken and Martin 2004, Wesolowski in review). Thus, in old forest systems, the role of several critical ecological and environmental factors such as food supply, predation and environmental conditions may be just as or more important than cavity availability in limiting cavity-nester densities (Walankiewicz 1991, Wesolowski and Stawarczyk 1991, Newton 1994, 1998, Lohmus and Remm 2005, Remm et al. 2006).

Table 2.1. Bird and mammal species nesting in excavated and non-excavated tree cavities, and percent of total cavities excavated by woodpecker and other excavator species in interior British Columbia, Canada, 1995-2006. See Table 1.2 for scientific names of species.

Species	**% nests in excavated cavities**	**% nests in non-excavated cavities**	**Total nests**	**% of cavities excavated (N=1371)**
Excavators				
Red-naped sapsucker	100	0	372	31
Red-breasted sapsucker	100	0	2	1
Downy woodpecker	100	0	63	5
Hairy woodpecker	100	0	74	6
American three-toed woodpecker	100	0	56	4
Black-backed woodpecker	100	0	4	2
Northern flicker	96	4	407	21
Pileated woodpecker	100	0	31	3
Black-capped chickadee	87	13	38	2
Red-breasted nuthatch	96	4	243	9
Unknown excavator	NA	NA	NA	13
Total Excavators	98	2	1290	
Secondary cavity-nesting birds				
Wood duck	100	0	1	
Bufflehead	97	3	58	
Barrow’s goldeneye	100	0	5	
Hooded merganser	100	0	1	
American kestrel	95	5	42	
Flammulated owl	100	0	1	
Northern hawk owl	0	100	2	
Northern saw-whet owl	100	0	17	
Tree swallow	91	9	307	
Mountain chickadee	93	7	295	1[a]
Mountain bluebird	86	14	253	
European starling	89	11	341	
Unidentified secondary cavity-nester	67	33	3	
Total secondary cavity-nester	90	10	1326	
Small mammals				
Northern flying squirrel	86	14	14	
Chipmunk	0	100	2	
Red squirrel	90	10	81	
Bushy-tailed woodrat	67	33	6	
Deer mouse	100	0	1	
Fisher	100	0	1	
Short-tailed weasel (ermine)	100	0	1	

Table 2.1, cont'd

Species	**% nests in excavated cavities**	**% nests in non-excavated cavities**	**Total nests**	**% of cavities excavated (N=1371)**
Unidentified small mammal	100	0	2	
Total small mammals	87	13	108	
Bark nesters				
Brown creeper *Certhia americana*	0	100	4	

[a] Two cavities were excavated by mountain chickadee, which we classify as a secondary cavity-nester as per Hill and Lein (1988)

Table 2.2. Linear mixed effects models predicting nest-site characteristics of cavity-nesting birds and mammals in interior British Columbia, Canada, between 1995-2006. Separate models were built for each of six nest-site characteristics, with cavity type ("excavated", "non-excavated") as the fixed effect, and individual cavity as the random effect. A positive estimate indicates that excavated cavities had a higher mean value than non-excavated cavities, and vice versa for negative estimates. Confidence intervals that do not encompass zero are highlighted in bold. See Table 1.2 for species scientific names.

Species	**Estimate (Excavated vs non-excavated)**	**SE**	**df**	**95% Confidence interval**
a) All species				
Cavity ht above ground (m) [a]	-0.61	0.08	1364	**(-0.77 – -0.45)**
Vertical depth (cm) [a]	0.23	0.20	664	(-0.16 – 0.62)
Internal diameter (cm)[b]	0.22	0.06	702	**(0.10 – 0.34)**
Entrance area (cm^2) [b]	0.51	0.10	709	**(0.31 – 0.71)**
Tree diameter at breast ht (cm) [b]	0.003	0.01	1653	(-0.02 – 0.03)
Distance to nearest edge (aspen groves) [a]	-0.15	0.27	438	(-0.68 – 0.38)
Distance to nearest edge (coniferous forest)	0.005	0.49	704	(-0.96 – 0.97)
b) Northern flicker				
Cavity ht above ground (m) [b]	-0.52	0.24	239	**(-0.99 – -0.05)**
Vertical depth (cm) [b]	0.30	0.13	155	**(0.05 – 0.55)**
Internal diameter (cm) [b]	-0.08	0.08	160	(-0.24 – 0.08)
Entrance area (cm^2) [b]	-0.01	0.10	159	(-0.21 – 0.19)
Tree diameter at breast ht (cm) [b]	-0.08	0.10	237	(-0.28 – 0.12)
Distance to nearest edge (aspen groves) [a]	0.26	0.61	139	(-0.94 – 1.46)
c) Mountain chickadee				
Cavity ht above ground (m)	0.32	0.93	186	(-1.50 – 2.14)
Vertical depth (cm)	3.89	1.67	88	**(0.62 – 7.16)**
Internal diameter (cm) [b]	-0.12	0.17	99	(-0.45 – 0.21)
Entrance area (cm^2) [b]	0.04	0.22	100	(-0.39 – 0.47)
Tree diameter at breast ht (cm) [b]	-1.04	2.30	184	(-5.55 – 3.47)
Distance to nearest edge (aspen groves)	24.0	8.37	23	**(7.59 – 40.4)**
Distance to nearest edge (coniferous forest)	-1.55	0.78	124	**(-3.08 – -0.02)**

Table 2.2, cont'd

Species	**Estimate (Excavated vs non-excavated)**	**SE**	**df**	**95% Confidence interval**
d) Mountain bluebird				
Cavity ht above ground (m)	-1.64	0.65	140	**(-2.91 – -0.37)**
Vertical depth (cm) [a]	0.42	0.40	101	(-0.36 – 1.20)
Internal diameter (cm)	1.48	1.03	108	(-0.54 – 3.50)
Entrance area (cm^2) [b]	0.34	0.18	111	(-0.01 – 0.69)
Tree diameter at breast ht (cm) [b]	0.20	0.09	137	**(0.02 – 0.38)**
Distance to nearest edge (aspen groves) [a]	0.02	0.48	100	(-0.92 – 0.96)
e) European starling				
Cavity ht above ground (m) [b]	-0.24	0.20	131	(-0.63 – 0.15)
Vertical depth (cm) [b]	-0.14	0.11	90	(-0.36 – 0.08)
Internal diameter (cm) [b]	0.15	0.10	93	(-0.05 – 0.35)
Entrance area (cm^2) [b]	-0.37	0.12	93	**(-0.61 – -0.13)**
Tree diameter at breast ht (cm) [b]	0.007	0.09	131	(-0.17 – 0.18)
Distance to nearest edge (aspen groves)	1.24	2.72	108	(-4.09 – 6.57)
f) Tree swallow				
Cavity ht above ground (m) [b]	-0.31	0.15	201	**(-0.60 – -0.02)**
Vertical depth (cm) [a]	0.49	0.32	118	(-0.14 – 1.12)
Internal diameter (cm) [b]	0.20	0.09	128	**(0.02 – 0.38)**
Entrance area (cm^2) [b]	0.55	0.16	128	**(0.24 – 0.86)**
Tree diameter at breast ht (cm) [b]	0.12	0.07	199	(-0.02 – 0.26)
Distance to nearest edge (aspen groves) [b]	0.07	0.46	122	(-0.83 – 0.97)

[a] Square-root transformed data used in analysis

[b] Log-transformed data used in analysis

Table 2.3. Characteristics of available excavated and non-excavated cavities surveyed in coniferous forests and aspen groves in 2000.

Variable	**Excavated** **Mean ± SE**	**Non-excavated** **Mean ± SE**	**Test statistic**[a]	***df***	***P***
Cavity ht above ground (m)	2.7 ± 0.1	2.7 ± 0.2	-0.29	198	0.8
Vertical depth (cm)[b]	24.4 ± 1.8	31.8 ± 6.9	-1.29	172	0.2
Internal diameter (cm)	13.2 ± 0.4	12.8 ± 1.1	0.40	180	0.7
Entrance area (cm^2)[c]	25.2 ± 1.0	38.2 ± 7.4	-1.20	178	0.2
Diameter at breast height (cm)[b]	34.2 ± 0.9	33.5 ± 3.1	1.30	197	0.2
Nearest edge (m)	25.7 ± 4.2	22.0 ± 7.4	2520.5	198	0.9

[a] Mann-Whitney *U* for nearest edge; Independent samples *t* for all others

[b] Log-transformed data used in analysis

[c] Square-root transformed data used in analysis

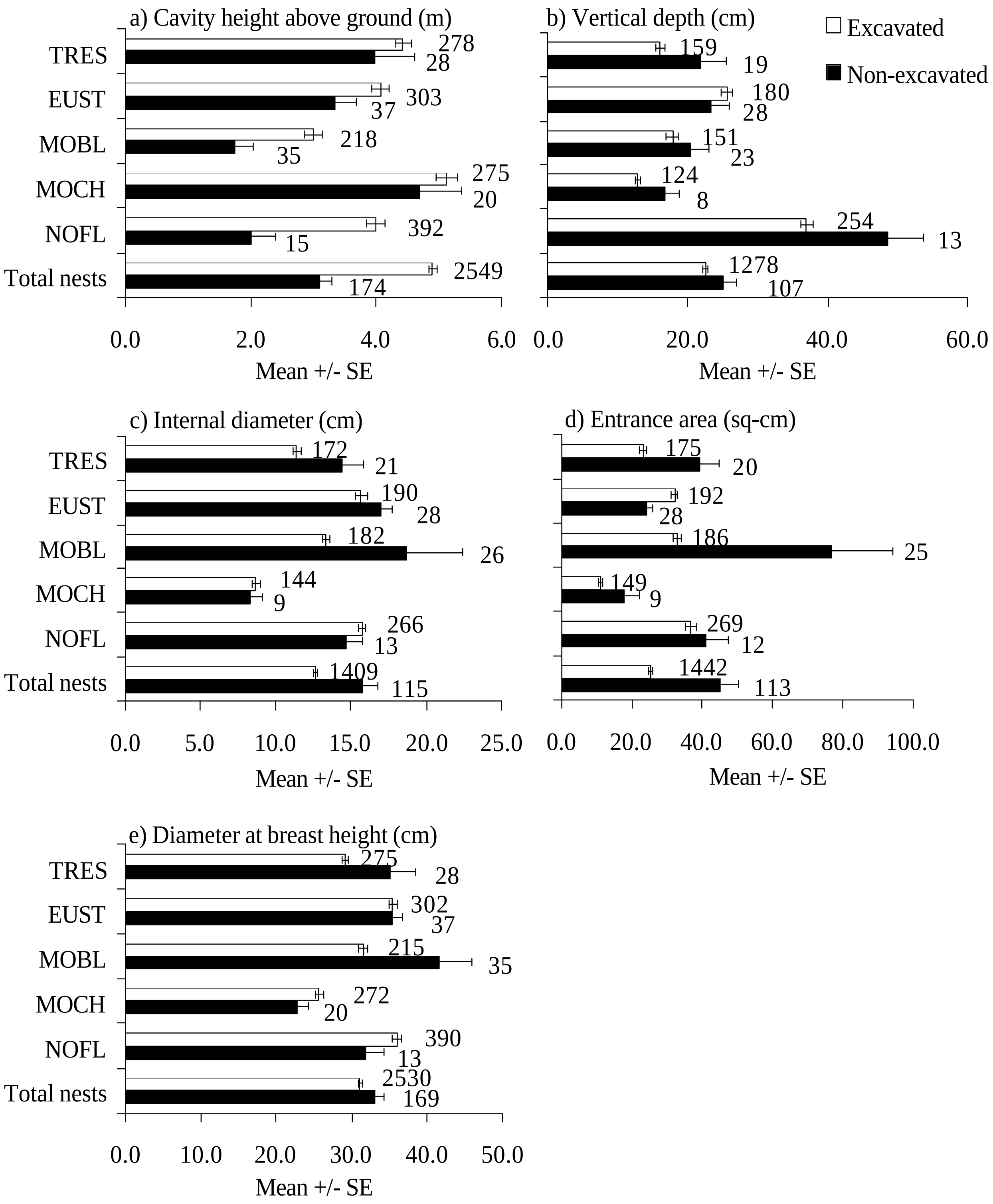


Figure 2.1. Characteristics of excavated and non-excavated cavities used by all species ("Total nests"), and by five individual species. See Table 1.2 for full species names, and Table 2.2 for results of mixed models analyses.

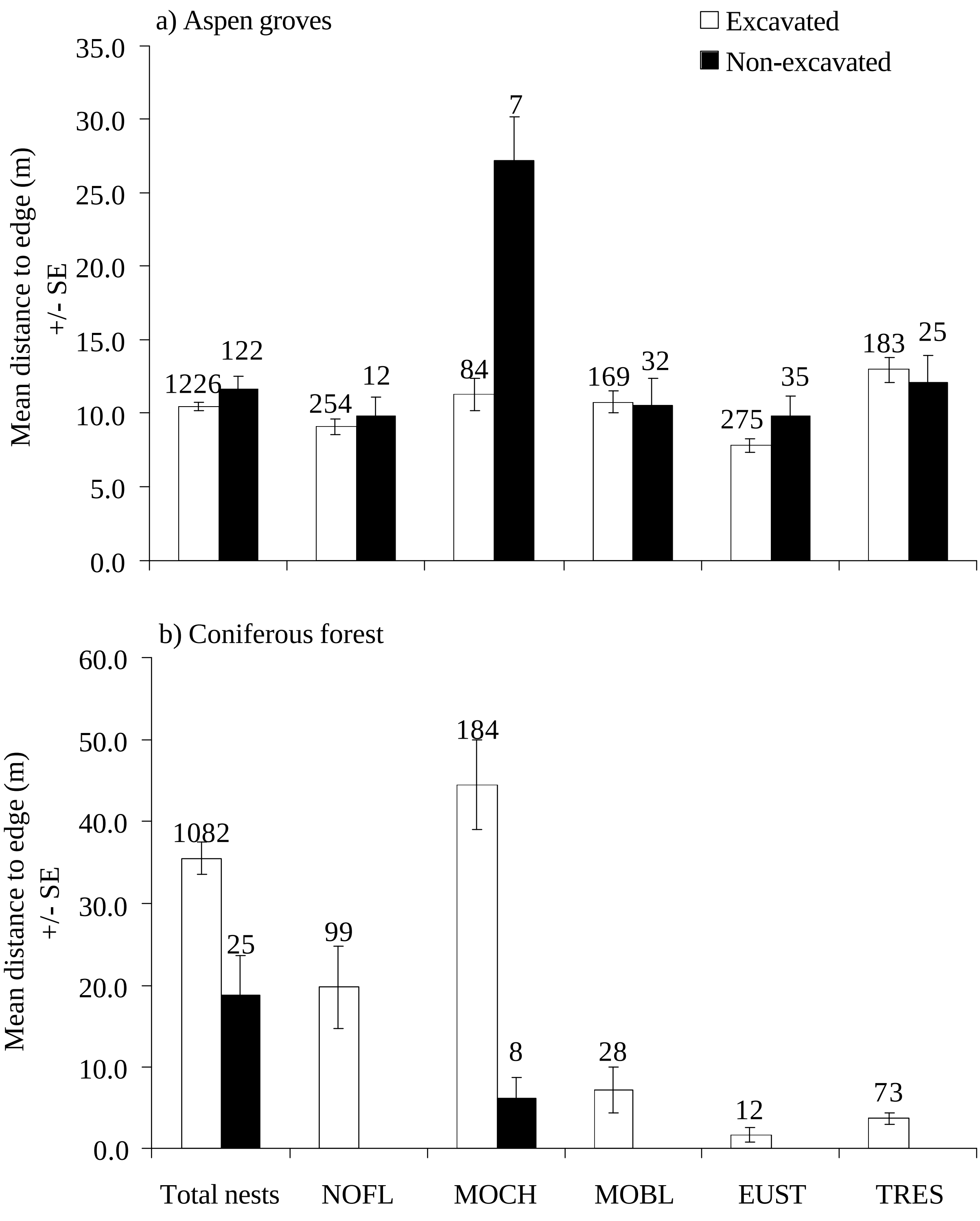
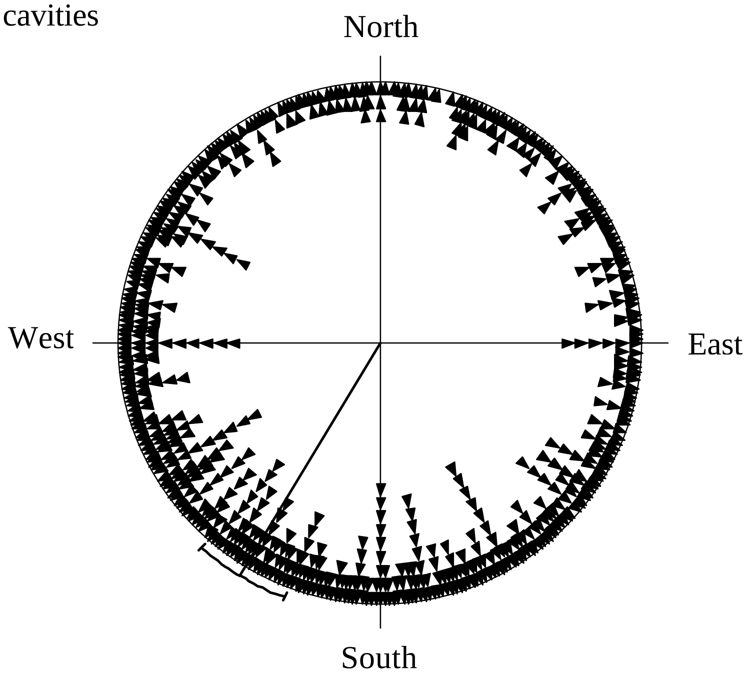


Figure 2.2. Distance of nests in excavated and non-excavated cavities to nearest edge in aspen groves and in coniferous forest sites. See Table 1.2 for full species names, and Table 2.2 for results of mixed models analyses.


a) Excavated cavities

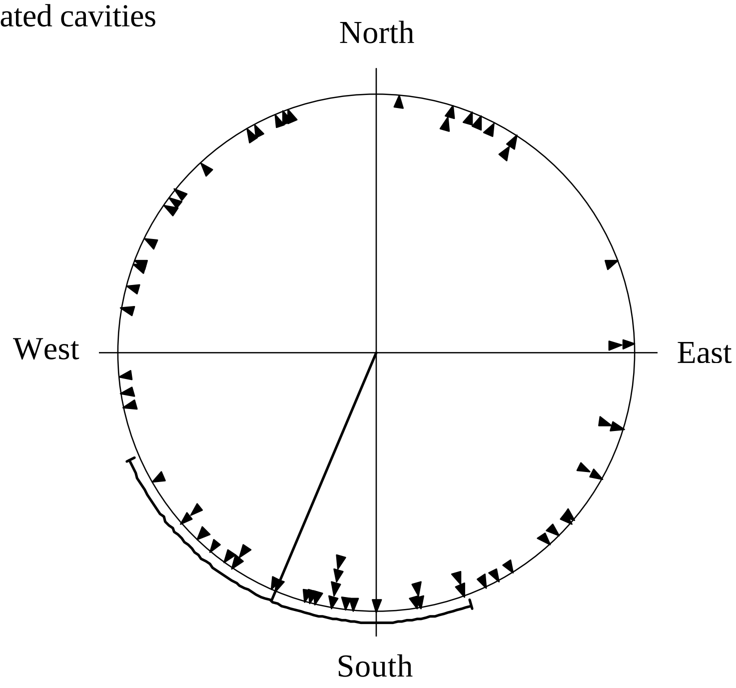

b) Non-excavated cavities

Figure 2.3. Orientation of a) excavated and b) non-excavated cavities. The arrow indicates mean orientation and the arcs to either side indicate the 95% confidence interval. See text for results of statistical tests.

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CHAPTER 3: DOES NEST-SITE AVAILABILITY LIMIT CAVITY-NESTERS IN MATURE FORESTS OF INTERIOR BRITISH COLUMBIA? A NEST BOX ADDITION EXPERIMENT.[2]

INTRODUCTION

Shelter availability limits populations of shelter-using species in a broad range of systems and taxa. Correlations between shelter availability and population density or survival, as well as experimental manipulations of essential resources, followed by an increase or decline in population or nest density, are often cited as evidence of resource limitation. Twig and stem-nesting ants, shell-using hermit crabs and fish, burrow-using hyrax (*Procavia capensis*), and salamanders that use small mammal tunnels or runways have all been shown to be limited by the availability of their respective shelters (Vance 1972, Fairall et al. 1986, Kuhlman 1994, Foitzik and Heinze 1998, Faccio 2003, Philpott and Foster 2005, Frederickson 2006). Cavity availability is the primary factor limiting breeding populations of many cavity-nesting birds and mammals (see review in Newton 1994, 1998). Circumstantial evidence that is often cited for nest-site limitation includes a high proportion of occupied cavities (e.g. Edington and Edington 1972, Robb et al. 1996, Bonar 2000, Bai et al. 2003) or a positive correlation between nest or breeding density and cavity or snag density (e.g. Raphael and White 1984, Zarnowitz and Manuwal 1985). Experiments that alter nest-site availability via nest box addition or removal, cavity blocking or creation, or snag removal or creation have provided direct evidence of nest-site limitation in numerous systems. For example, Brawn and Balda (1988) observed an increase in breeding densities of pygmy nuthatches (*Sitta pygmaea*), western bluebirds (*Sialia mexicana*) and violet-green swallows (*Tachycineta thalassina*) after box addition on three treatment sites in

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[2] A version of this chapter will be submitted for publication.
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Arizona. Density of Eurasian kestrels increased after box provisioning in rural farmland habitat in Spain (Fargallo et al. 2001). Population levels of several woodpecker and secondary cavity-nesting species were negatively impacted by removal of snags in pine (*Pinus* spp.) forests of South Carolina and Arizona, as well as in burned mixed conifer forests in California (Scott 1979, Raphael and White 1984, Lohr et al. 2002).

Most studies on cavity-nester population limitation have been conducted in harvested forests, in which natural rates of cavity creation and loss have been altered (Newton 1994, 1998). Most of these studies showed an increase in breeding densities following addition of nest boxes to second-growth forest (e.g. Brawn and Balda 1988, Caine and Marion 1991, Holt and Martin 1997). The few studies conducted in mature or old growth forests suggest that cavity-nesters in undisturbed habitat may be limited by factors other than cavity availability (Gauthier and Smith 1987, Waters et al. 1990, Newton 1994, 1998). In Brawn and Balda's study cited above, nesting densities only increased in treatment sites consisting of young, thinned stands and not in an older forest site. Walankiewicz (1991) found that secondary-cavity nester breeding densities in old growth forests in Poland were limited by predation rather than nest-site availability. In interior British Columbia, Gauthier and Smith (1987) found that territorial behaviour rather than cavity availability limited bufflehead (*Bucephala albeola*) density. In mature forests with a full complement of excavators and a variety of cavity types, food availability, predation pressure and other social or environmental factors may replace cavity availability as the main drivers of population limitation (Martin and Norris 2007).

There is conflicting evidence for the cavity limitation hypothesis in mature mixed conifer forests of interior British Columbia. While cavity densities were low in the region (<2 cavities/ha), cavity occupation rates were also low (<10%/year; Aitken 2002), suggesting that the few cavities present may have been of insufficient quality for some secondary users, possibly because they were of unsuitable size, were located in suboptimal habitat, or had other features that made them undesirable. For example, large-bodied cavity-nesters, such as small mammals, ducks, and raptors, rely primarily on cavities created by large excavators, which may be less abundant in the landscape than smaller cavities (Van Balen et al. 1982, Eadie et al. 1998, Martin et al. 2004). Additionally, in an earlier study in the area, I found that stand-scale features such as tree density and proximity to edge influenced nest-site preferences of some cavity-nesters more than cavity or tree characteristics (Aitken 2002, Aitken and Martin 2004). While cavities in general were distributed evenly with respect to edge and interior (Aitken 2002), excavated cavities in coniferous forests were significantly farther from edge than non-excavated cavities (Chapter 2, Figure 2.2), suggesting that cavity quality may vary spatially across the landscape. Thus, cavity quality and location may be more important in limiting cavity-nesting populations than overall cavity abundance (Lohmus and Remm 2005).

The objective of my study was to determine whether cavity availability and location limit cavity-nesting populations in mature coniferous forests in interior BC. I conducted a nest box addition experiment in which I increased overall nest-site availability in mature coniferous forest sites with low cavity densities and low occupation rates. Boxes were designed to simulate cavities created by the most common small-bodied and medium-large bodied excavators in the community in order to determine whether low cavity occupancy rates in coniferous forests were due to a lack of excavated cavities with those size characteristics. Additionally, boxes were placed in edge and interior habitat to ascertain whether a low abundance of excavated cavities in edge habitats was limiting cavity-nester populations. I predicted that if cavities were limiting for cavity-nesters in coniferous forests, an increase in nest-site availability via box addition would result in an increase in nest density of cavity-nesting species. I predicted that if availability of large-sized cavities or excavated cavities in edge habitats were limiting for some cavity-nesters, there would be preferential use of large boxes, and boxes in edge habitats.

METHODS

Study Area

Research was conducted in seven coniferous forest study sites (Doc English Lake, MacIntyre Lake, Military Gate, Rock Lake, Solitary Woods, Tongue, The Y; Chapter 1, Figure 1.2) between May and July 1996-2006. See Chapter 1 for a detailed description of the study area.

Nest monitoring and box addition experiment

I utilized a replicated before-after/control-impact (BACI) experimental design (Underwood 1992, 1994), in which I monitored cavities for six years pre-treatment, two years during treatment (box addition), and three years following box removal on three treatment sites (one treatment site, Doc English, was not monitored in 2006) and four control sites. All previously active nest trees were marked with numbered aluminum tags and previously active cavities were assigned identifying numbers as part of a larger cavity-nester study operating on the study area since 1995 (Martin and Eadie 1999). From 1 May – 31 July, previously active and newly excavated cavities were monitored approximately twice per week. Cavities were checked with a flashlight and mirror and were considered active nests if they contained at least one egg or nestling. I also recorded cavities used for nesting or roosting by small mammals (Martin et al. 2004).

In late July 2001, nest boxes were added to three coniferous forest study sites (Doc English, MacIntyre Lake, and Military Gate; Chapter 1, Figure 1.2). These were sites that had low densities of cavities (1.9 cavities/ha) between 1996-2001, and low nest densities, with cavity occupation rates of <10% per year (Aitken 2002). Boxes were removed in late July 2003, and I continued to monitor nesting in cavities during the 2004-2006 breeding seasons.

Two sizes of nest boxes were used to simulate small and medium-large sized cavities. Thirty-five small-sized boxes were constructed from downed aspen trees, cut into sections approximately 0.5 m long. Sections were hollowed out using a chisel and entrance holes were drilled in each box using a circular saw with a 3.5 cm-diameter blade (9.6 cm^2 entrance area). Pieces of plywood were attached to the tops of boxes using screws, which could be loosened in order to open the boxes to view the nest contents. Box measurements were: vertical depth $\bar{x} = 17.8 \pm 0.72$ cm, internal width $\bar{x} = 8.2 \pm 0.39$ cm, and entrance area $\bar{x} = 12.8 \pm 0.46$ cm^2. These boxes fell within the range of measurements of cavities created or used by the small-bodied cavity excavators in the study area, such as downy woodpeckers (*Picoides pubescens*), black-capped chickadees (*Poecile atricapillus*), and red-breasted nuthatches (*Sitta canadensis*; Martin et al. 2004). Thirty-five standard rectangular, top-opening plywood boxes were used to simulate cavities created or used by the main larger-bodied cavity excavators in the area, including northern flicker, hairy woodpecker and red-naped sapsucker (Martin et al. 2004). Box measurements were: vertical depth = 23.0 cm, internal width = 23.4 cm, entrance area = 38.5 cm^2.

Five pairs of boxes (1 small, 1 large) were placed in the forest interior (>100 m from nearest edge) at each of the three sites, five pairs were placed near grassland edge at two of the sites (<15 m from edge; Doc English, Military Gate), and five pairs were placed near pond edge at two of the sites (<15 m from edge; Doc English, MacIntyre Lake). Boxes within pairs were placed an average of 10m apart and box pairs were spaced an average of 50m apart. Mean height above ground was 3.4 ± 0.1 m for small boxes and 3.3 ± 0.1 m for large boxes. Boxes were nailed to aspen or conifer trees randomly.

Data analyses

I examined the effect of box addition on total nest density of all cavity-nesting species, and on four species for which sufficient sample sizes were available (mountain chickadee, red-breasted nuthatch, red squirrel, northern flying squirrel). Chickadee nest densities across years on treatment and control sites were examined using linear mixed effects models, and nuthatch and squirrel densities were examined using generalized linear mixed-effects models with a penalized quasi-likelihood method of parameter estimation (glmmPQL). GlmmPQL is an appropriate statistical analysis when dependent data follow a Poisson distribution, as was the case with my nuthatch and squirrel density data (Breslow and Clayton 1993, Nelson and Leroux 2006). All analyses were performed in the statistical package R (R version 2.4.0, R Development Core Team 2006). Treatment type (box addition or control) and period ("pre-treatment": 1996-2001; "during treatment": 2002-2003; and "post-treatment": 2004-2006) were fixed effects, site was a random effect, and square-root transformed nest (or nest and roost) density was the dependent variable. I compared proportions of edge and interior boxes used by mountain chickadees, red squirrels and flying squirrels using Fisher's Exact tests (for chickadees in 2002 and 2003, and for squirrels in 2002), and chi-squared tests (for squirrels in 2003).

RESULTS

Nest box addition resulted in a 300% increase in nest-site availability on coniferous forest sites, from a mean of 1.2 cavities per hectare before box addition to 3.5 cavities or boxes per hectare with box addition. Cavity-nesting birds and small mammals used 51% of large boxes for nesting or roosting in 2002 and 67% in 2003. Occupancy of small boxes was similar in both years (37% in 2002, 34% in 2003). The majority of occupied large-sized boxes were used for roosting by small mammals, while small-sized boxes had similar proportions of nests and roosts. In both treatment years, mountain chickadees used boxes in forest interior slightly less than expected from their availability, and used boxes near wet edge more than expected, with both trends being much stronger in 2003 than in 2002 (Figure 3.1a; Fisher's Exact Test, 2002: $P = 0.10$, 2003: $P = 0.008$). While nesting and roosting red squirrels and northern flying squirrels preferred boxes near wet edge and avoided boxes in forest interior in 2002, these preferences switched in 2003 (Figure 3.1b; Fisher's Exact Test, 2002: $P = 0.02$, chi-squared test, 2003: $X^2 = 3.1$, df = 2, $P = 0.22$). Chewing by squirrels significantly enlarged the entrances of 23 out of 35 small-sized boxes between 2002-2003 (paired samples *t*-test: $t = -4.03$, df = 35, $P < 0.001$), resulting in a mean entrance area of 14.0 cm^2 for small boxes in 2003, compared to a mean of 12.8 cm^2 in 2002.

Total density of bird and mammal nests on treatment sites more than tripled in 2002, remained at that level in 2003, and decreased by 35% (from 2003 levels) in 2004 after boxes were removed (Table 3.1, Figure 3.2a). Despite a slight increase in nest density in 2005 due to an increase in woodpecker nests on treatment sites, total nest densities returned to near pre-treatment levels in 2006. The proportion of nests in boxes was 30% of 27 nests in 2002 and 36% of 25 nests in 2003.

The increase in total nest density after box addition was largely accounted for by a significant increase in mountain chickadee (MOCH) nests on treatment sites (Table 3.1). MOCH nest density increased nearly nine-fold (from 0.04/ha to 0.37/ha) on treatment sites in 2002, remained high in 2003, decreased by 55% in the first year following box removal, and returned to pre-treatment levels in 2006 (Figure 3.2b). The proportion of MOCH nests in boxes increased from 46% of 13 nests in 2002 to 64% of 11 nests in 2003, but this was not significant ($X^2 = 0.73$, df = 1, n = 24, $P = 0.39$). All MOCH nests were in small-sized boxes.

Squirrel nest and roost density increased significantly following box addition, and dropped to pre-treatment levels immediately following box removal (Table 3.1, Figure 3.2c). Nearly all squirrel nests and roosts were in boxes (75% of 16 boxes used in 2002 and 85% of 27 used in

2003). Red squirrels preferred large over small boxes in both years (all of 8 boxes used in 2002, and 92% of 13 used in 2003), while flying squirrels preferred small boxes in 2002 (3 of 4 nests/roosts) and large boxes in 2003 (8 of 10 nests/roosts).

Interestingly, although only one red-breasted nuthatch pair nested in a box (in 2003), box addition appeared to have a positive effect on nuthatch nest densities on treatment sites (Table 3.1). While sample sizes were low, nuthatch nest density in cavities doubled (from 0.11/ha to 0.2/ha) on treatment sites in 2002, remained high in 2003 and 2004, and returned to pre-treatment levels in 2005 and 2006 (Figure 3.2d).

DISCUSSION

Numerous studies have examined limitation of cavity-nesting populations by nest-site availability in North America and Europe. Newton (1994) provided a comprehensive review and concluded that while nest-sites may limit populations in harvested forests, other factors may be more important in limiting cavity-nester densities in mature forests where natural processes of cavity creation and decay have not been altered. In the 13 years since his review was published, there have been few nest-site limitation experiments in unharvested or mature forests reported in the literature. Lohr et al. (2002) found a reduction in woodpecker breeding territories in experimental sites in which snags were removed. Common goldeneye (*Bucephala clangula*) nest density increased following box addition in Finnish forests (Poysa and Poysa 2002), as did densities of mountain chickadees, pygmy nuthatches, and house wrens (*Troglodytes aedon*) after box addition in Colorado (Bock and Fleck 1995). Many recently published studies have cited circumstantial evidence, such as an abundance of unoccupied holes, to support the contention that cavities may not be limiting in mature forest. To my knowledge, my study is the only recent long-term, replicated nest box addition experiment with before and after treatment data for cavity-nesters in mature mixed conifer forests.

The most abundant secondary cavity-nesters on my treatment sites, mountain chickadees, red squirrels and northern flying squirrels, accounted for 37% of cavity nests (n = 131) on the treatment sites over the course of the study, and these three species were the most affected by box addition. While I observed a few nests of mountain bluebirds, tree swallows, and bufflehead (*Bucephala albeola*) in cavities before and after my box addition experiment, I did not record any nests of these species in boxes or cavities during the treatment period. Bluebirds and swallows are usually associated with aspen groves surrounded by grassland in the study area (Chapter 1), and my coniferous forest sites may not have provided adequate access to foraging habitat for these species (Robertson et al. 1992, Power and Lombardo 1996). Bufflehead appear to prefer cavities excavated by flickers in my study area, and these may be more abundant in aspen groves than in coniferous forest (Aitken et al. 2002, Martin et al. 2004). Additionally, species occurring at low densities may take longer to locate and use boxes added to sites (Brawn and Balda 1988).

Response of mountain chickadees to box addition

Mountain chickadee density appeared to be influenced by nest-site availability on my study sites, as suggested by a significant increase in nest density following box addition. As well, MOCH only used small-sized boxes. In a larger study in the area, presented in Chapter 2, nearly all MOCH nests for which hole origin could be determined were in cavities excavated by small to medium-bodied species such as red-breasted nuthatch (34%), red-naped sapsucker (26%), and downy woodpecker (13%). However, the majority of cavities in the study area were excavated by larger-bodied woodpeckers, such as northern flickers, hairy woodpeckers, and pileated woodpeckers (Aitken 2002). As well, MOCH nest cavity volume and entrance size, which may influence reproductive success, predation and competition (Zeleny 1978, Moeed and Dawson 1979, van Balen 1984, Slagsvold 1989, Robertson and Rendell 1990; but see Wiebe 2001) were strongly scaled with chickadee body size (Martin et al. 2004), suggesting that chickadees select nest cavities within an optimal size range. Breeding density of MOCH increased significantly on my treatment sites after the addition of nest boxes within this size range, suggesting that natural cavities with these characteristics may be limited on my study sites.

Previous studies found conflicting evidence of nest-site limitation in MOCH, and suggested that the importance of cavity availability in limiting MOCH populations may depend on stand age and food availability (Dahlsten and Copper 1979, Brawn and Balda 1988, Bock and Fleck 1995). In my study area, there was a concurrent outbreak of two preferred chickadee foods, western spruce budworm (*Choristoneura occidentalis*; Heppner and Turner 2006) and mountain pine beetle (*Dendroctonus ponderosae*; Martin et al. 2006). The increase in food resources across the study area may have allowed chickadees to respond to the experimental increase in nest-site availability on my treatment sites. Chickadee nest density also increased on control sites, but the smaller magnitude of the increase compared to treatment sites suggests that other factors such as nest-site availability limited the degree to which chickadees were able to respond to the increase in food availability. If food rather than nest sites primarily limited chickadees, I would have expected a comparable increase in populations across all my study sites, regardless of box addition. This was not the case, leading me to conclude that nest-site availability, rather than food availability, was the main factor limiting MOCH density in my study area.

Because I added boxes to treatment sites at the end of July 2001, MOCH had a full winter to assess the increased availability of nest sites prior to the first breeding season of the experiment. Adult MOCH spend the winter in foraging flocks in home ranges encompassing several breeding territories (McCallum et al. 1999), allowing them to evaluate nest-site availability through the non-breeding season. As well, local populations include non-breeding “floaters”, subordinate adults that acquire territories as more dominant individuals die or shift to higher quality territories (Hogstad 1989, Smith 1984, 1989, Mostrom et al. 2002). The increase in nest-site availability via box addition may have provided breeding opportunities for non-breeding floaters in the MOCH population on my treatment sites. It is unlikely that the increase in MOCH nest density was simply due to adults switching from nearby breeding territories to those with boxes as in that case I should have observed a concurrent decline in cavity use within my treatment sites, and no overall increase in nest density. Additionally, many species show an inverse relationship between resource density and territory size (Village 1983, Marshall and Cooper 2004). The increase in nest-site availability on my treatment sites may have resulted in a reduction in territory size among dominant MOCH, allowing floaters to settle in boxes or cavities that might otherwise have been unavailable to them.

Response of red squirrels and northern flying squirrels to box addition

Red squirrel and northern flying squirrel nest and roost densities increased considerably following box addition on my sites and subsequently crashed when boxes were removed, suggesting that squirrels were limited by nest-site availability. However, previous studies have found that while arboreal squirrels (*Tamiasciurus* spp. and *Glaucomys* spp.) readily use nest boxes, this does not always result in an increase in total population size or the proportion of adults breeding (Brady et al. 2000, Carey 2002, Ransome and Sullivan 2004), and that squirrels are primarily limited by food availability (Sullivan 1990, Ransome and Sullivan 1997, 2004). In addition to using cavities, red squirrels and northern flying squirrels construct bolus nests in the tree canopy, and therefore they may not be dependent on cavities as nest and roost sites (Young et al. 2002, Ransome and Sullivan 2004). Because I did not assess squirrel density directly through live trapping and monitoring of breeding adults, I do not know whether total population levels increased following box addition. However, while most cavities in my sites were excavated by larger-bodied woodpecker species, total cavity densities were low (Aitken 2002), and the dramatic increase in squirrel nest and roost density, the preference for large-sized boxes, and enlargement of the entrances of smaller boxes by squirrel chewing, suggests that there may be a shortage of suitable large-sized den sites in the study area. Young et al. (2002) found an inverse relationship between cavity availbility and red squirrel use of alternate den sites, and thus, it is possible that the apparent increase in squirrel densities on my treatment sites was due to a shift from bolus nests to boxes. Further research on squirrel productivity and survival is necessary to determine whether these populations are limited by nest-site availability in mature forests of interior BC.

Response of red-breasted nuthatches to box addition

The increase in red-breasted nuthatch density on treatment sites in my study may have been due to over-winter habitat assessment by nuthatches. Like chickadees, nuthatches are residents that spend the winter in the vicinity of their summer breeding range and can assess resource availability throughout the year, allowing them to select breeding territories accordingly (Matthysen et al. 1992, Ghalambor and Martin 1999). For example, during the mountain pine beetle outbreak in my study area, nuthatches switched from aspen-dominated nest patches to those containing high densities of beetle-infested pine (Norris 2007). While nuthatches are able to excavate cavities, soft decayed trees may be limited in the landscape (Steeger and Hitchcock 1998, Schepps et al. 1999, Brandeis et al. 2002, Lohr et al. 2002), excavation itself may be energetically costly (Wiebe and Swift 2001), and it can take up to two weeks to complete a cavity (Ghalambor and Martin 1999). Thus, nuthatches often utilize existing holes rather than excavating a new cavity, and approximately 40% of nuthatch nests are in old cavities on my study sites (Aitken et al. 2002, Wiebe et al. 2006). As well, where nest-site availability is low, interspecific competition for cavities may be intense. Therefore, it is possible that nuthatches assess territory and habitat quality partially on the basis of cavity abundance, which may indicate not just the presence of suitable nest-sites but also the potential level of interspecific competition for those cavities. Thus, while only one nuthatch pair nested in a box on my treatment sites, the experimental increase in nest-site availability may have enhanced overall habitat quality for nuthatches, leading to an increase in nuthatch breeding densities in cavities in those sites.

Conclusions

Despite low cavity occupancy rates prior to nest-site supplementation in my study sites at Riske Creek, nest and roost densities increased following box addition. I suggest that the availability of suitable nest and den sites may be limiting for some cavity-nesting populations in these mature coniferous forests, and that cavity size and location may influence the true availability of cavities in the landscape.

Table 3.1. Mixed models predicting density of a) all nests of cavity-nesting birds and mammals, b) mountain chickadee nests, c) red squirrel and northern flying squirrel nests and roosts, and d) red-breasted nuthatch nests in relation to treatment type (box addition or control) and treatment period (pre-treatment, during treatment or post-treatment). Linear mixed effects (LME) models were used to examine chickadee density, while generalized linear mixed-effects models (GLMM) were used to examine nuthatch and squirrel densities. LME and GLMM calculate separate parameter estimates for each level of categorical fixed effects, and report estimates in relation to the first level specified in the data alphabetically. Thus, parameters were calculated in relation to Treatment type = "Box addition" and Period = "During treatment ". For example, the significant negative parameter estimate for total bird and mammal nests in the pre-treatment period indicates that nest density was significantly lower in that period than during treatment. Site was included in the model as a random effect.

Parameter	**Estimate**	**SE**	**df**	***t*-statistic**	***P***
a) Total cavity-nesting birds & mammals					
Intercept	0.75	0.082	65	9.23	<0.0001
Period: Pre-treatment	-0.59	0.068	65	-8.69	<0.0001
Period: Post-treatment	-0.25	0.078	65	-3.19	0.002
Treatment type: Control	-0.46	0.11	5	-4.24	0.008
Period: Pre-treatment *Treatment type: Control	0.46	0.090	65	5.09	<0.0001
Period: Post-treatment *Treatment type: Control	0.22	0.10	65	2.15	0.04
b) Mountain chickadee					
Intercept	0.35	0.040	65	8.73	<0.0001
Period: Pre-treatment	-0.32	0.039	65	-8.05	<0.0001
Period: Post-treatment	-0.18	0.045	65	-4.01	0.0002
Treatment type: Control	-0.19	0.054	5	-3.49	0.02
Period: Pre-treatment *Treatment type: Control	0.19	0.052	65	3.64	0.0005
Period: Post-treatment *Treatment type: Control	0.12	0.059	65	2.05	0.04

Table 3.1, cont'd.

Parameter	**Estimate**	**SE**	**df**	***t*-statistic**	***P***
c) Red squirrel and northern flying squirrel					
Intercept	-0.23	0.23	65	-1.01	0.32
Period: Pre-treatment	-4.67	0.79	65	-5.91	<0.0001
Period: Post-treatment	-2.55	0.43	65	-5.90	<0.0001
Treatment type: Control	-3.57	0.74	5	-4.81	0.005
Period: Pre-treatment *Treatment type: Control	4.85	1.11	65	4.38	<0.0001
Period: Post-treatment *Treatment type: Control	3.48	0.88	65	3.93	0.0002
d) Red-breasted nuthatch					
Intercept	-1.77	0.28	65	-6.38	<0.0001
Period: Pre-treatment	-1.15	0.35	65	-3.27	0.002
Period: Post-treatment	-0.84	0.41	65	-2.07	0.04
Treatment type: Control	-1.11	0.48	5	-2.31	0.07
Period: Pre-treatment *Treatment type: Control	0.46	0.59	65	0.78	0.44
Period: Post-treatment *Treatment type: Control	0.48	0.66	65	0.73	0.47

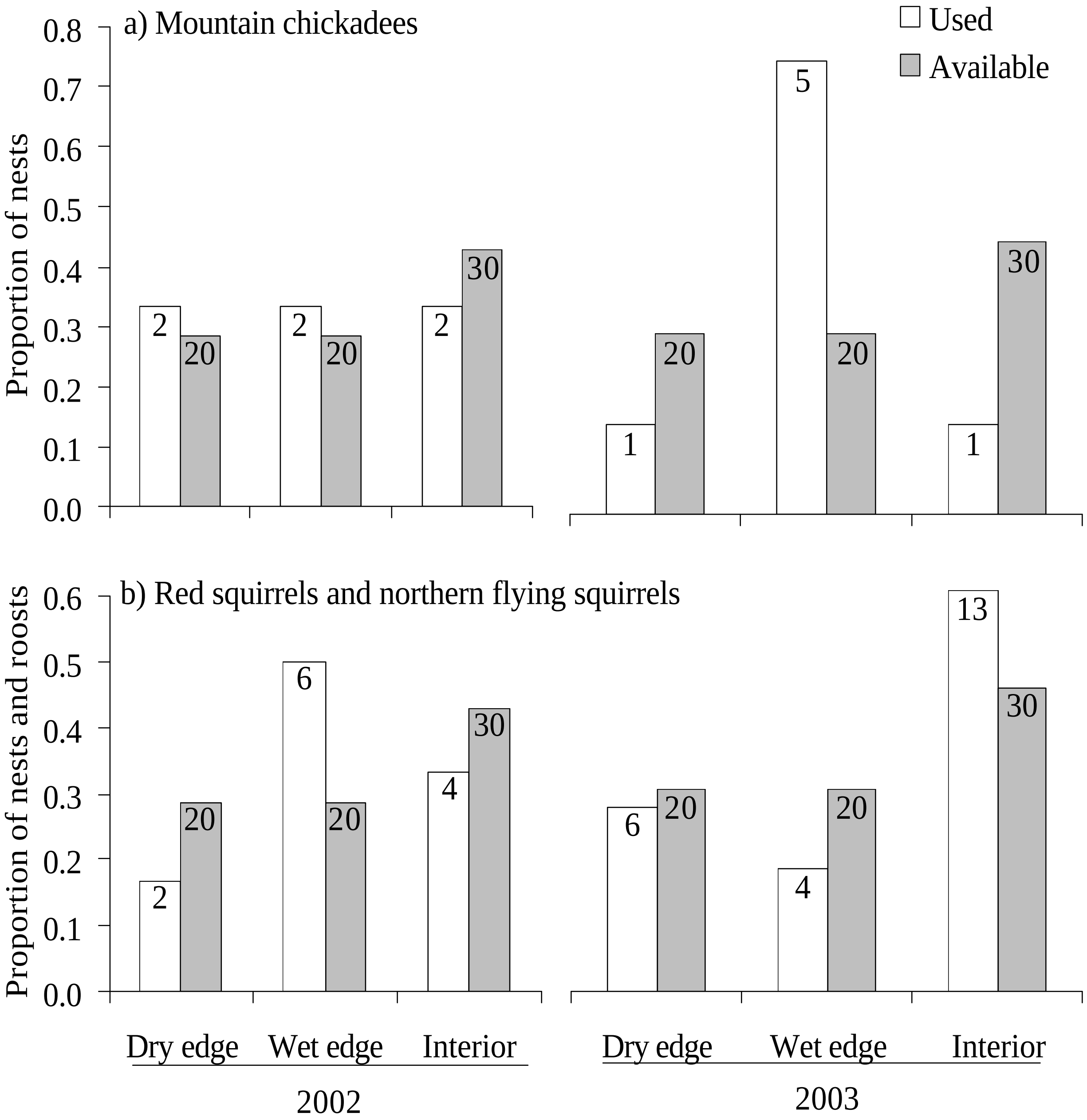

Figure 3.1. Proportion of boxes used by a) mountain chickadees, and b) red squirrels and northern flying squirrels compared to proportion of boxes available in dry grassland edge, wet (lake) edge, and forest interior on treatment (box addition) sites in 2002 and 2003. See text for results of Fisher's Exact and chi-square tests.

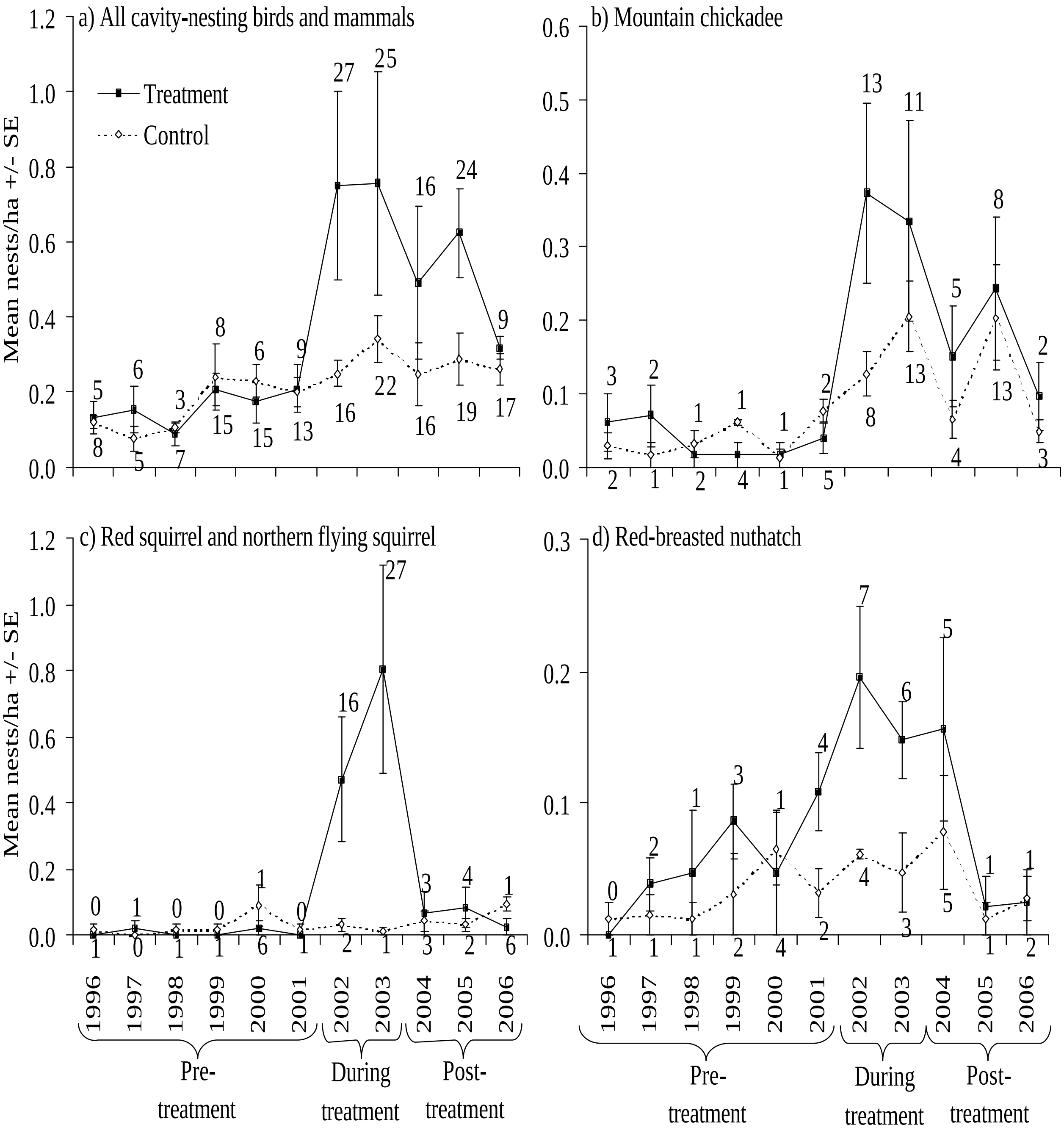

Figure 3.2. Density of cavities or boxes occupied by a) all cavity-nesting bird and mammal species, b) mountain chickadees, c) red squirrels and northern flying squirrels (nests and roosts), and d) red-breasted nuthatches on treatment (boxes added) and control sites. Numbers above error bars are the total active nests on treatment sites, and numbers below bars are the total active nests on control sites. See text for details of statistical analyses.

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CHAPTER 4: RESPONSE OF SECONDARY CAVITY-NESTERS TO AN EXPERIMENTAL REDUCTION IN CAVITY AVAILABILITY: RESOURCE SELECTION PLASTICITY AND SPECIES INTERACTIONS.[3]

INTRODUCTION

Cavity-nesting communities, which are structured hierarchically based on production of and competition for suitable cavities, are comprised of species that range in their degree of nest-site specialization and dominance (Martin and Eadie 1999). Nesting resources may be limited or unpredictable for these species (Newton 1994) and individuals that are able to exploit a range of nest sites may have greater opportunities for breeding than individuals that are restricted in their nest-site requirements. Secondary cavity-nesting species, which cannot excavate their own cavities, rely on cavities created by woodpeckers or on a limited number of naturally occurring non-excavated cavities, and while landscape-level cavity abundance may be relatively stable, there may be considerable local variation in cavity availability and quality (Aitken and Martin 2004, Aitken and Martin, in review). Thus, cavity-nesting communities provide an opportunity to study the effects of changes in resource availability on species across a range of resource acquisition strategies.

Resource selection plasticity and behavioural dominance may influence a species' ability to respond to temporal and spatial changes in resource availability, particularly if dominant species have highly specialized resource requirements. Subordinate species with more generalized resource preferences than dominant species may be better able to withstand stochasticity in resource availability (Pimm and Pimm 1982, Palmer 2003). Additionally, plasticity in nest-site selection may allow individuals to utilize a broader range of habitat types, and to reduce nest

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predation and interspecific competition (Albano 1992, Cuervo 2004, Forstmeier and Weiss 2004, Eggers et al. 2006). Thus, the extent to which natural and human-induced environmental variability impact community structure and stability may be influenced by the ecological plasticity of component species (Brown et al. 2001, Hooper et al. 2005, Richmond et al. 2005).

Cavity density in mature aspen (*Populus tremuloides*) groves in the Cariboo-Chilcotin region of British Columbia, Canada, averages 16/ha with overall occupancy rates of 35-44% (Aitken 2002, Aitken and Martin 2004). However, occupancy rates of individual cavities vary, as some cavities are occupied every year while others are occupied only sporadically (Aitken et al. 2002). Among "high occupancy" cavities (those occupied annually or biannually), cavity nesters exhibited preferences related to cavity age, size and proximity to edge (Aitken et al. 2002, Aitken and Martin 2004). Thus, while nest sites may appear to be abundant, individual species' preferences may influence true nest-site availability.

Using a cavity blocking experiment, I altered the availability of high occupancy cavities in order to: a) examine changes in nesting abundance at the cavity-nester community- and species-levels in response to changes in the availability of an essential resource, tree cavities, and b) determine whether secondary cavity-nesters in a natural landscape with an apparent abundance of cavities were, in fact, nest-site limited. I predicted that if nest-site availability were limited for some species in this community, nest abundance of these species would be correlated with changes in cavity abundance.

METHODS

Study area

Research was conducted between 2000-2005 in 20 aspen groves (0.1-1.7 ha each), each spaced 16-222 m from the nearest grove or forest and dominated by trembling aspen, with varying amounts of lodgepole pine and Douglas-fir. See Chapter 1 for a complete study area description.

Nest monitoring and cavity blocking experiment

I utilized a replicated before-after/control-impact (BACI) experimental design (Underwood 1992, 1994), in which I monitored cavities for two years prior to treatment (cavity blocking), two years during treatment, and two years following cavity reopening in seven treatment aspen groves and 13 control groves. All previously active nest trees were marked with numbered aluminum tags and previously active cavities were assigned identifying numbers as part of a larger cavity-nester study operating on the study area since 1995 (Martin and Eadie 1999). From 1 May – 31 July, previously active and newly excavated cavities were monitored approximately twice per week. Cavities were checked with a flashlight and mirror and were considered active nests if they contained at least one egg or nestling. I also recorded cavities used for nesting by small mammals (Martin et al. 2004).

In April 2002, prior to the start of the breeding season, I blocked all high occupancy cavities (those that had been occupied in the previous two years; Aitken et al. 2002) on treatment sites using plastic garden mesh stapled over the cavity entrance. I blocked 36 of 80 cavities on treatment sites (45%), representing 30-80% of cavities in each aspen grove. However, five blocked cavities were repeatedly chewed open by small mammals and, thus, were considered as unblocked in subsequent analyses. Overall, cavity blocking resulted in a 47% decrease in cavity abundance, from a pre-treatment mean of 27.9 cavities/ha to 14.8 cavities/ha during treatment. I removed the blocking material in late July 2003, and continued to follow nesting on all 20 sites during the 2004 and 2005 breeding seasons.

Data analyses

I examined the effect of cavity blocking on nest abundance of all cavity-nesting birds and mammals, and three secondary cavity-nester species for which sufficient data were available (≥

10 nests per year): European starling, mountain bluebird and tree swallow. I used generalized linear mixed-effects models using a penalized quasi-likelihood method of parameter estimation in the statistical package R (glmmPQL; R version 2.4.0, R Development Core Team 2006). GlmmPQL is an appropriate statistical analysis when dependent data follow a Poisson distribution, as was the case with my nest abundance data **(**Breslow and Clayton 1993, Nelson and Leroux 2006**)**. Treatment type (cavity blocking or control) and period ("pre-treatment": 2000-2001; "during treatment": 2002-2003; and "post-treatment": 2004-2005) were fixed effects, site was a random effect, and nest abundance was the dependent variable.

RESULTS

Cavity blocking resulted in a significant decline in overall abundance of cavity nesters (Table 4.1). Total abundance of bird and mammal nests on treatment sites decreased by 41% in 2002 and a further 13% in 2003, resulting in a total decrease in nest abundance of 49% over the two treatment years (Figure 4.1a). Total nest abundance returned to near pre-treatment levels in 2004 (Figure 4.1a).

The decline in total nest abundance after cavity blocking was largely accounted for by a significant decline in European starling (the most abundant secondary cavity-nester) nests on treatment sites (Table 4.1). Starling nests decreased by 72% on treatment sites in the first year after blocking (2002) and a further 60% in 2003, resulting in a total decrease of 89% in abundance in the two years cavities were blocked (Figure 4.1b). There was a corresponding increase in starling nest abundance on control sites in the second treatment year (2003). After blocking materials were removed from cavities, starling nest abundance did not return to pre-treatment levels, and remained lower on treatment sites than on controls in both 2004 and 2005.

Cavity blocking had a significant positive effect on mountain bluebird nest abundance, with an increase in nest numbers beginning in the second year of cavity blocking and continuing until the end of the study (Table 4.1, Figure 4.1c). Tree swallow nest abundance was not significantly affected by cavity blocking, although there was a slight increase in abundance on control sites in 2004 after cavities were reopened (Figure 4.1d).

DISCUSSION

At the community level, cavity-nesting bird and mammal populations decreased following cavity blocking and returned to pre-treatment levels following cavity reopening, suggesting that the cavity-nesting community as a whole was limited by cavity abundance. However, species-level resistance to fluctuations in resource availability appeared to play a role in driving the community-level response. Species with generalist nest cavity preferences, such as bluebirds and swallows, displayed high resistance in nest abundance following the experimental decrease in cavity availability, while the most dominant, specialist cavity-nester, European starling, displayed low resistance and resilience to cavity blocking. Generalist species may be better able to withstand stochasticity in resource availability than specialists (Pimm and Pimm 1982, Palmer 2003), while specialists may put more effort into acquiring a limited number of higher quality resources.

Response of European starlings to cavity blocking

Abundance of starlings declined significantly immediately after cavity blocking and did not recover after cavities were reopened. Interestingly, all seven starling nests in my treatment sites in 2002 and 2003 were in the only remaining cavities with characteristics similar to cavities previously occupied by starlings on those sites (K. E. H. Aitken and K. Martin, unpublished data). Thus, it appears that starlings selected all the preferred remaining cavities and, once those were occupied, remaining breeders moved to other aspen groves rather than occupying less suitable cavities within treatment sites. A slight increase in starling nest abundance on nearby control sites in the second treatment year may support this hypothesis. Although starlings are considered nest-site generalists because they have adapted successfully to nesting in both natural and human-made structures, nest-site selection studies suggest that they have specialized nest-site preferences. In Poland, starlings had stronger preferences for nesting cavities based on tree species, height above ground, and cavity entrance shape than did most other species in the community (Wesolowski 1989). Starlings in the Netherlands and Sweden preferred cavities that were large internally (van Balen et al. 1982, Carlson et al. 1998). Earlier, I found that starlings preferred nest-sites that were larger internally, closer to grassland edge, and in trees with only one cavity (Aitken and Martin 2004). Starlings in urban areas of Ontario used a smaller range of human-made structures for nesting and with a narrower range in characteristics than did another introduced secondary cavity-nester, the house sparrow (*Passer domesticus*; Savard and Falls 1981). Lohmus and Remm (2005) suggested that availability of high quality nest-sites, as opposed to total cavity abundance, may limit some populations of secondary cavity-nesters. My results suggest that starling populations may be limited by the availability of suitable cavities with a relatively narrow range of preferred characteristics.

Studies have noted a delayed response of some secondary cavity-nesters to changes in nest site availability (Brawn and Balda 1988), particularly among species that prospect for nest-sites for use in subsequent years (Eadie and Gaulthier 1985, Stutchbury and Robertson 1987, Holt and Martin 1997, Poysa and Poysa 2002). Non-breeding starlings (floaters) prospect for cavities for the following year by examining cavities occupied by conspecifics, particularly during the nestling period (Tobler and Smith 2004). This may explain the sustained negative impact of cavity blocking on starling nest abundance. Floaters that prospected for cavities on my treatment sites in 2001 (prior to cavity blocking) may have overestimated cavity availability for the following year, while birds prospecting in 2003 may have underestimated cavity availability for 2004. Additionally, because starlings are semi-colonial and may use conspecific breeding activity as an indicator of nest-site suitability (Tobler and Smith 2004), the low densities of breeders on the treatment sites in 2002 and 2003 may have dissuaded other starlings from returning to those sites in subsequent years, regardless of cavity availability in 2004 and 2005.

Response of mountain bluebirds and tree swallows to cavity blocking

Overall, mountain bluebird and tree swallow nest abundances were not affected negatively by the experimental reduction in cavity availability in this study. Both species are secondary cavity-nesters that co-occur with a range of other cavity-nesting species in a variety of habitats throughout North America and display generalist nest-site preferences (Robertson et al. 1992, Power and Lombardo 1996). I found that in addition to tree cavities, bluebirds and tree swallows used cavities in downed trees, crevices behind bark, hollow stumps, cracks in boulders, and even metal bridge pieces for nesting (Martin et al. 2004, Aitken and Martin, in review). Plasticity in nest-site selection may have enabled bluebirds and tree swallows to respond quickly to the experimental changes in cavity availability in my study.

Role of interspecific dominance in species' responses to cavity blocking

Cavity blocking resulted in an increase in mountain bluebird nest abundance in the second year of the experiment and continued for at least two years after cavities were reopened. This increase appeared to correspond with the decrease in starling abundance, suggesting that bluebird populations may be limited by starling presence, either through aggressive interactions or through exploitation competition (Ingold 1994, Sara et al. 2005). I suspect the latter because starlings initiate nesting approximately 1-2 weeks earlier on average than do bluebirds (K. Martin, unpublished data) and I have never observed direct aggression between the two species on my sites. Previous studies showed that the presence of starlings may influence nest-site selection and timing of breeding by some native cavity-nesters (Kerpez and Smith 1990, Pell and

Tidemann 1997, Ingold 1998, Fisher and Wiebe 2006). For example, Davis et al. (1986) found that starlings exclude bluebirds from potential nest sites through their earlier timing of breeding or that bluebirds initiate nesting later to avoid competition with starlings. When nesting in areas with starlings, eastern bluebirds (*Sialia sialis*) nested in cavities with smaller entrances than in areas without starlings (Pinkowski 1976). Mountain bluebirds shifted to smaller and deeper cavities after starlings became established in central British Columbia in the 1960s (Peterson and Gauthier 1985). Plasticity in nest-site selection and nesting phenology may allow bluebirds to coexist with and avoid direct competition with starlings.

Starlings are considered to be aggressive competitors in North America, Australia and other regions where they have been introduced, with potentially detrimental effects on populations of native cavity-nesters (Kerpez and Smith 1990, Cabe 1993, Pell and Tidemann 1997). However, starlings may not be as adaptable and resilient as they are generally considered given recent declines in starling populations in Europe, possibly due to changes in agriculture and loss of foraging habitat (Rintala et al. 2003, Svensson 2004, Laiolo 2005, Robinson et al. 2005). A review of North American Breeding Bird Survey and Christmas Bird Count trends found no evidence that starlings have severely impacted populations of cavity-nesters since their introduction (Koenig 2003). Pimm and Pimm (1982) suggested that behaviourally dominant species are more likely to be affected by disturbance than are subordinates, if the dominant species is restricted to higher quality resources while the subordinates are capable of using poorer resources. My results suggest that inflexibility in starling nest-site preferences, and plasticity in nest-site preferences and nesting phenology of native cavity-nesting species, may enable coexistence of starlings with native species.

Experiments on population limitation in cavity-nesters

To my knowledge, the cavity blocking experiment presented here is the first involving a replicated before-after/control-impact (BACI) design with multiple treatment and control sites, several years of data, and involving multiple species. Most studies of population limitation in cavity-nesters involve addition or removal of nest boxes, and very few studies have experimentally reduced or increased the availability of natural cavities. In one of the few studies involving artificial cavity excavation, Walters et al. (1992) found an increase in breeding territory abundance of red-cockaded woodpeckers (*Picoides borealis*) after drilling cavities in live pine (*Pinus* spp.) trees in North Carolina. A few studies found that removal of all snags in experimental plots resulted in a reduction in cavity-nester breeding densities but these studies did not address cavity availability directly (Scott 1979, Raphael and White 1984, Lohr et al. 2002). The few studies that involved cavity blocking experiments lacked long-term data or adequate replication (e.g. Brush 1983, Waters et al. 1990). Breeding biology and nest predation risk may differ between birds nesting in boxes versus natural cavities (Nilsson 1984, Robertson and Rendell 1990, Kuitunen and Aleknonis 1992, Purcell et al. 1997, Wesolowski and Stanska 2001, Evans 2002). Thus, cavity blocking experiments may provide a more accurate reflection of population responses to variation in resource availability. While experiments that alter the availability of natural cavities may be logistically more difficult than nest box experiments, these methods deserve consideration by researchers examining population limitation in cavity-nester communities.

Conclusions

Ecological plasticity may allow species to withstand or even benefit from environmental stochasticity and to cope with interspecific competition (Ostfeld and Keesing 2000, Moreno et al. 2001, Yang 2004). However, plastic or generalist species may face trade-offs between using abundant but low quality resources versus rare high quality resources (Abrams 1990). For secondary cavity-nesters such as bluebirds and tree swallows, selecting an abundant but low-quality cavity may reduce competition and energy spent on searching for a nest-site, but may also result in lower reproductive success if that cavity is more vulnerable to predation, is not close to optimal foraging habitat, or has poor thermal qualities (Slagsvold 1986, Sedgeley 2001, Lohmus 2003, Lohmus and Remm 2005). Conversely, secondary cavity-nesters that select a more rare but higher quality cavity may suffer reproductive costs if they expend more energy in locating or defending that nest-site than in egg-laying, incubation or parental care (Duckworth 2006). Cavity-nesters with less plastic nest-site preferences or in habitats with a dearth of cavities may simply defer breeding if suitable high quality nest-sites are not available (Holt and Martin 1997). Further studies on trade-offs in resource availability and quality for cavity-nesters, and resource partitioning by cavity-nesters, will allow for a better understanding of the mechanisms of species coexistence in these communities.

Table 4.1. Generalized linear mixed models (GLMM) predicting abundance of a) total bird and mammal cavity nests, b) European starling nests, c) mountain bluebird nests, and d) tree swallow nests in relation to treatment type (cavity blocking or control) and treatment period (pre-blocking, during blocking or post-blocking). GLMM calculates separate parameter estimates for each level of categorical fixed effects, and reports estimates in relation to the first level specified in the data alphabetically. Thus, parameters reported here were calculated in relation to Treatment type = “Blocking” and Period = “During blocking ”. For example, the significant positive parameter estimate for total bird and mammal nests in the pre-blocking period indicates that nest abundance was significantly higher in that period than during treatment. Site was included in the model as a random effect.

	a) Total birds and mammals					**b) European starling**				
Parameter	**Estimate**	**SE**	**df**	***t***	***P***	**Estimate**	**SE**	**df**	***t***	***P***
Intercept	1.06	0.20	96	5.18	<0.0001	-1.30	0.54	96	-2.42	0.02
Treatment type: control	0.47	0.25	18	1.89	0.07	1.37	0.63	18	2.17	0.04
Period: Pre-blocking	0.57	0.15	96	3.72	0.0003	1.52	0.35	96	4.40	<0.0001
Period: Post-blocking	0.50	0.15	96	3.24	0.002	-0.15	0.46	96	-0.33	0.7
Period: preblocking * Treatment type: control	-0.57	0.18	96	-3.12	0.002	-1.31	0.39	96	-3.36	0.001
Period: post-blocking * Treatment type: control	-0.55	0.18	96	-2.97	0.004	-0.05	0.50	96	-0.10	0.9

	c) Mountain bluebird					**d) Tree swallow**				
Parameter	**Estimate**	**SE**	**df**	***t***	***P***	**Estimate**	**SE**	**df**	***t***	***P***
Intercept	-0.62	0.36	96	-1.73	0.09	-0.66	0.45	96	-1.45	0.2
Treatment type: control	0.17	0.43	18	0.39	0.7	0.23	0.55	18	0.42	0.7
Period: Pre-blocking	-0.29	0.39	96	-0.73	0.5	0.00	0.35	96	0.00	1.0
Period: Post-blocking	0.69	0.32	96	2.20	0.03	0.20	0.34	96	0.59	0.6
Period: preblocking * Treatment type: control	0.34	0.45	96	0.74	0.5	-0.08	0.41	96	-0.19	0.8
Period: post-blocking * Treatment type: control	-0.80	0.39	96	-2.02	0.046	-0.09	0.39	96	-0.23	0.8

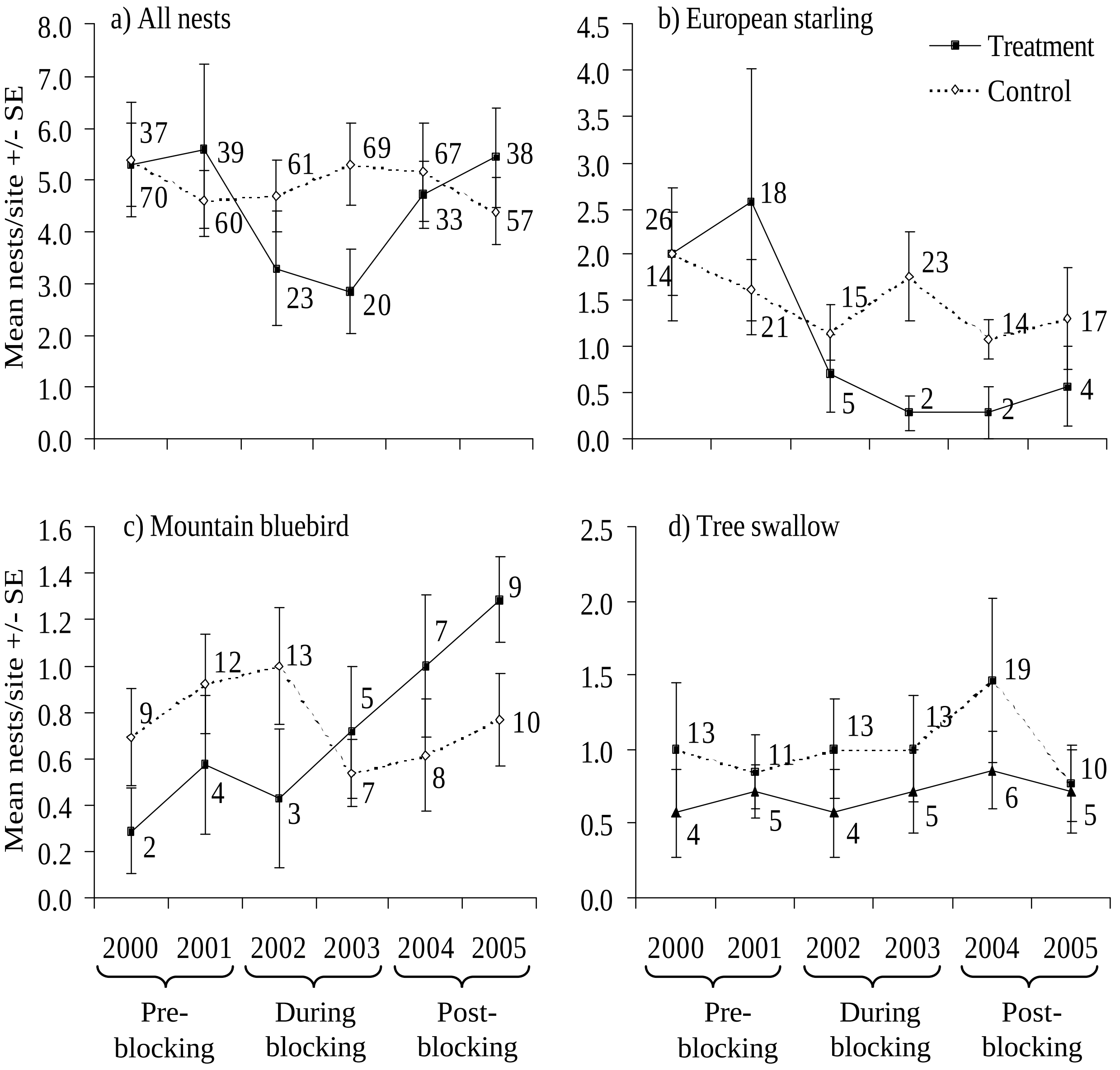

Figure 4.1. Mean nest abundance of a) all cavity-nesting birds and mammals, b) European starlings, c) mountain bluebirds, and d) tree swallows on 7 treatment (cavity blocking) and 13 control sites at Riske Creek, BC. Sample sizes shown beside points are the total sample of nests.

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CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

THESIS SUMMARY

Nest cavities created by woodpeckers or natural decay processes are an essential commodity for secondary cavity-nesting species. In harvested forests, some populations of cavity-nesters may be limited by the availability of suitable cavities (Newton 1994). Additionally, woodpeckers are often considered keystone species in forest systems because they can influence the diversity and abundance of other cavity-nesters in the community (Daily et al. 1993, Mikuskinski and Angelstam 1997, Martin and Eadie 1999, Aubry and Raley 2002, Duncan 2003). However, little is understood about the relative importance of excavated versus non-excavated holes for cavity-nesters, and the role of nest-site availability in limiting populations across different forest types and conditions (Martin and Wesolowski, in review). It has been suggested that in mature forests, with a full complement of excavators and undisrupted processes of cavity creation and loss, factors other than cavity availability may limit populations of cavity-nesters (Waters et al. 1990, Walankiewicz 1991, Newton 1994, Martin et al. 2004).

My study showed that, while cavities created by woodpeckers and other excavators were considerably more abundant in coniferous forests and aspen groves of Becher's Prairie, BC, most secondary cavity-nesters used them at random relative to their availability (Chapter 2). In mature coniferous forests, mountain chickadee nest density appeared to be limited by cavity availability, and there appeared to be a shortage of large-sized den sites for red squirrels and northern flying squirrels (Chapter 3). Cavity availability appeared to limit the abundance of nesting European starlings in mature aspen groves, while starling abundance appeared to limit mountain bluebird nest abundance (Chapter 4). My results suggest that the sizeable and diverse assemblage of excavators on Becher's Prairie may contribute to the high abundance of cavities in the area, but that these cavities vary in suitability and quality for secondary cavity-nesters.

Additionally, for some species such as bluebirds, cavity availability may be limited indirectly, via exploitative competition from other species. Thus, cavity-nester populations may be influenced by the abundance and distribution of cavities, but responses are modulated by cavity-nester community dynamics. Further research into intra- and interspecific partitioning of nest-sites, and the influence of competition and predation from small mammals using cavities, will help to elucidate mechanisms of species coexistence in these complex communities. Below, I highlight some knowledge gaps in cavity-nesting community ecology and suggest directions for future research.

KNOWLEDGE GAPS AND SUGGESTIONS FOR FUTURE RESEARCH

Intra- and interspecific partitioning of cavities

The influence of cavity creation rates and longevity on niche partitioning in cavity-nesting communities is poorly understood. While resource abundance, predictability and seasonality can affect resource partitioning and competition (Tilman 1982, Giller 1984), few studies of community structure examine relationships with resource availability and suitability (Giller 1984, Pulliam 2000). The predictability of a resource may influence the ability of species to specialize on that resource, and high predictability favours smaller niche breadths (Cody 1974). Conversely, high resource seasonality or turnover favours broader niches. Individual nest cavities may persist in the landscape for several years and may be reused multiple times by various occupants both within and across years (Aitken et al. 2002). However, disease and stage of tree decay influence excavation activities by woodpeckers and weak excavators (Harestad and Keisker 1989, Schepps et al. 1999), which in turn influences the types of holes excavated and the rate of hole creation (McLaren 1962, Conner et al. 2001). Additionally, as cavities age, they may decay, become filled with nest material, be enlarged by woodpeckers or squirrels (Conner et al. 2001, Chapter 3), or be destroyed during nest predation attempts (DeWeese and Pillmore

1972, Aitken, personal obs.). Long-term cavity monitoring studies are needed in order to determine the influence of cavity creation, longevity, and loss on cavity-nesting community structure and dynamics.

Resource availability and limitation are primary factors influencing niche partitioning (Hutchinson 1957, Pulliam 2000). Many studies have examined the influence of interspecific competition on resource selection and niche partitioning in a variety of species, including desert ants (*Aphaenogaster* spp.), geese (*Anser* spp.), warblers (*Vermivora* spp.) and tits (*Parus* spp.; Herrera 1978, Madsen 1985, Sanders and Gordon 2000, Martin and Martin 2001). However, most of these studies focused on closely related species, which presumably overlap considerably in most aspects of their life history, such as foraging and nesting niches. Shelter-using communities, in contrast, provide an opportunity to study resource use and niche partitioning among diverse groups of species or taxa, which may only overlap in one portion of their total niche, reducing the relative amount of overlap in total niche space among the species in the community. Because tree holes are essential for reproduction in cavity-nesters and, therefore, are likely to be a primary resource for which species compete, cavity-nesting communities provide an excellent system in which to examine resource partitioning across taxa and trophic levels.

Few studies have directly examined nest-site partitioning in cavity-nesting communities. Peterson and Gauthier (1985) compared nest cavity characteristics of several species in interior British Columbia seven years and 25 years after European starlings reached the area. They found that mountain bluebirds shifted to deeper nest cavities, while northern flickers shifted to narrower cavities. Several researchers have suggested that some cavity nesters use small diameter cavities to avoid competition with European starlings for larger holes (Peterson and Gauthier 1985, Rendell and Robertson 1989). For example, Dobkin et al. (1995) found that tree swallows nesting in preferred starling habitat close to woodland edge only used small red-naped sapsucker cavities. Swallows nesting >15 m from edge shifted to northern flicker cavities. Similarly, Pinkowski (1976) found that eastern bluebirds nesting in areas with starlings used cavities with smaller entrances than in areas without starlings. However, most of these studies were short-term or hampered by small sample sizes, and none examined the impact of niche shifts on reproductive success of cavity nesters.

Long-term, large-scale community-level studies of nest-site selection in relation to changes in cavity availability and population densities of potential competitors are necessary to understand resource partitioning in cavity-nesting communities. Specifically, there is a need for studies examining how species with overlapping nest-site requirements partition cavities temporally and spatially, and how morphological and life history factors of cavity-nesting species influence niche breadth, overlap and flexibility. Niche partitioning and flexibility may be examined by comparing relative resource use among populations of species under varying habitat, temporal and competitive conditions (Llewellyn and Jenkins 1987, Kildaw 1999).

Influence of competition and predation by small mammals on cavity availability and selection

Few studies have examined the influence of small mammals on nest-site availability and selection in cavity-nesting communities. In Europe, several species of dormouse (Family Gliridae) are nest-site competitors and predators of cavity-nesting birds (Juskaitis 2006), and have been shown to influence nest-site availability and selection for other species in the community (Sara et al. 2005). On Becher’s Prairie, red squirrels, northern flying squirrels, bushy-tailed woodrats, weasels (*Erminea* spp.), marten and fisher (*Martes* spp.), and deer mice use cavities for nesting, roosting, food storage and other activities. Because these species are resident throughout the year, they may influence availability and quality of nest-sites in several ways. In Chapter 3, I showed that chewing of box entrances resulted in a significant increase in entrance size, and most boxes and cavities used by squirrels were filled with nest material such as grass, moss and lichen, possibly reducing cavity useability for other species. Cavities may also be filled with winter food caches, rendering them unuseable for other cavity-nesters in the spring if the stores have not been depleted. This impact may be particularly significant for migratory birds that arrive in spring after small mammals, which begin breeding as early as March, have occupied preferred cavities, especially for medium to large-bodied birds that use cavities in the same size range as squirrels. Finally, in addition to competing with other cavity-nesters for nest-sites, most of these small mammal species prey on cavity-nesting adults, eggs or nestlings (Robertson et al. 1992, Power and Lombardo 1996, Bradley and Marzluff 2003). This interesting dynamic is largely unexplored in these communities as small mammals tend to be under-sampled or not monitored in many cavity-nester studies, and their role in cavity-nesting community ecology requires further examination.

Predation risk can influence nest-site selection (Martin and Roper 1988, Hogstad 1995, Eggers et al. 2006), and a better understanding of the predator assemblage is needed for the cavity-nesting community of Becher's Prairie. Currently, only anecdotal evidence exists regarding which species prey on adults, juveniles, nestlings or eggs of cavity-nesters in this region. Black bears (*Ursus americanus*) prey on nests of flickers and cavity-nesting ducks in the Cariboo-Chilcotin (Walters and Miller 2001, Evans et al. 2002, K. L. Wiebe, unpublished data). Identification of hairs left at the entrances of some depredated nests suggests that red squirrels, flying squirrels and marten (*Martes americana*) prey on eggs, nestlings and possibly adults in cavities (Evans et al. 2002, Mahon and Martin 2004, K. E. H. Aitken and K. Martin, unpublished data). Other potential nest predators recorded in the area include weasels (*Mustela* spp.), marten and fisher (*Martes* spp.), chipmunks (*Eutamius* spp.), American Crows (*Corvus brachyrhynchos*), and carpenter ants (*Camponotus* spp; Kilham 1971, Keisker 1987, Power and Lombardo 1996, Martin et al. 2006). Several woodpeckers, including northern flickers and pileated woodpeckers, prey on eggs and nestlings of cavity-nesters (Loftin and Leeds 1981, Robertson et al. 1992, Christman and Dhondt 1997). Understanding predation pressures will help explain nest-site selection patterns in cavity-nesting communities, and shed light on whether a high abundance of unused cavities in the landscape indicates that nest-sites are not limiting for cavity-nesters, or whether an excess of unoccupied holes is a strategy by cavity-nesters to reduce predation risk by increasing search times of predators (Watts 1987, Martin and Roper 1988).

Summary

The role of nest-site availability in limiting cavity-nesting populations in mature forests, and the importance of woodpeckers as cavity providers, may depend on the abundance and quality of non-excavated holes, as well as the cavity and habitat attributes associated with the woodpecker species present. On my study sites in interior British Columbia, woodpeckers created the majority of cavities in the landscape but these were not selected preferentially by secondary cavity-nesters and instead were used in proportion to their abundance. Thus, while woodpeckers may play a role in providing a copious supply of cavities in this system, many of the secondary cavity-nesters in the community are not solely reliant on excavated holes for nesting. Additionally, while nest-sites may initially appear to be abundant and potentially non-limiting at the community level, individual species preferences, as well as interspecific interactions, may influence true nest-site availability.

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