NEST-SITE AVAILABILITY, SELECTION AND REUSE IN A CAVITY-NESTING COMMUNITY IN FORESTS OF INTERIOR BRITISH COLUMBIA

By

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ABSTRACT

Cavity nesting communities are structured in a complex hierarchy of interdependencies based on the creation of and competition for nest-sites. This structure has been called a nest web. Although cavities are persistent and may be used multiple times, few studies have examined cavity use in relation to availability, or patterns of nest-site reuse. My objectives were to: 1) determine cavity availability and use in continuous and naturally-fragmented forests, and 2) examine nest-site reuse by cavity nesting guilds and species.

To examine cavity availability and use, I measured nest-site characteristics in continuous forests and naturally-fragmented aspen (*Populus tremuloides*) stands in British Columbia. I examined cavity selection at the community, guild and species levels using resource selection indices. Continuous forests had fewer cavities and lower cavity occupancy rates (9-10%) than fragments (35-44%). However, cavity characteristics did not differ between those habitats. Overall, cavity nesters preferred live, unhealthy trees with few holes. Nest-site selection was influenced by tree and habitat attributes, rather than cavity characteristics such as orientation. Low overall occupancy rates suggested that there was a surplus of cavities.

To examine nest-site reuse, 193 cavities were monitored between 1995-1999. Eight percent of cavities were destroyed during the study, mainly due to tree blowdown. Cavities were occupied two years in a row, rather than intermittently. Reuse rates were highest for cavities occupied by secondary cavity nesters (48%) and were lowest for those used by weak excavators (17%). Although woodpeckers were the main providers of cavities for secondary cavity nesters in the community, only 28% of cavities used by woodpeckers were occupied the following year. Reuse rates varied considerably among species within all guilds. Deep cavities with large entrances and those in aspen were reused most often, as were those in aspen groves and close to forest edges.

I suggest that large-scale attributes such as proximity to foraging habitat are better indicators of nest-site suitability than microhabitat characteristics. Thus cavity-nesting communities should be managed at a larger scale than individual nest trees or cavities. Because cavity abundance does not reflect cavity suitability, counts of holes will not predict the ability of a habitat to sustain cavity-nester populations.

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PREFACE

A version of Chapter 3 of this thesis was published in The Auk 119(2): in press. The title is "Nest site reuse patterns for a cavity-nesting bird community in interior British Columbia". The co-authors of this paper were Dr. Kathy Martin and Dr. Karen L. Wiebe. K.E.H. Aitken performed all analyses and wrote the manuscript. Preliminary data analysis, assistance with writing the first draft of the manuscript, and general editorial assistance were provided by the co-authors.

Dr. Kathy Martin: ____________________________________

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Chapter 1:
General Introduction and Thesis Overview

Use of shelters such as tree cavities, burrows and shells is common in many taxa. One or a few species create these resources, which are then used by others. For example, soft-bodied hermit crabs (Anomura: Superfamily Paguroidea) require empty gastropod shells for shelter (Hazlett 1981). Golden-Shouldered Parrots (*Psephotus* spp.), caimans (*Paleosuchus* spp.), African Giant Rats (*Cricetomys gambianus*), and Eumenid wasps (Hymenoptera: Eumenidae) nest in or on termite mounds, which provide heat and cover (Ajayi 1977, Batra 1979, Weaver 1982, Magnusson et al. 1985). Prairie Dog (*Cynomys* spp.) burrows provide shelter and nest sites for Burrowing Owls (*Athene cunicularia*) and for other birds, reptiles, amphibians and mammals (Clark et al. 1982, Desmond and Savidge 1996). Availability of shelters limits some populations of secondary users (Vance 1972, Newman 1987, Newton 1994). Inter- and intraspecific competition for these resources results in niche or resource partitioning in these communities (Abrams et al. 1986, Lindenmayer et al. 1991, McCallum et al. 2001). The costs and benefits of acquiring or defending resources provided by other species in the community results in patterns of trophic structure and function similar to those found in food webs.

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 80 bird and 20 mammal species in North America use tree cavities (Burt and Grossendeider 1980, Ehrlich et al. 1988). Their communities are structured in a nest web of interdependencies based on nesting, foraging and other interactions (Martin and Eadie 1999). Woodpeckers, or primary cavity excavators (PCE), create holes that are used by secondary cavity nesters (SCN). SCNs are 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. Weak cavity excavators (WCE), including nuthatches (*Sitta* spp.) and some chickadees (*Poecile* spp.), either excavate a cavity on their own or enlarge a hole begun by a PCE. Facultative cavity nesters, including Great Horned Owls (*Bubo virginianus;* Houston et al. 1998) and Pacific-slope Flycatchers (*Empidonax difficilis;* Lowther 2000), use either tree holes or open nests. Little is understood about the costs and benefits of cavity use for these species.

Woodpeckers are considered keystone species in forest communities and can influence the diversity and abundance of other cavity nesters in the community (Daily et al. 1993, Martin and Eadie 1999).

Cavity-nesters make up 30-65 percent of the forest-dwelling species of birds and mammals in forests of the Pacific Northwest (Bunnell and Kremsater 1990). Because they depend on trees for nesting and other activities, they are considered sensitive to forest removal (Angelstam and Mikusinski 1994, Newton 1994). 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 forests because they are more susceptible to windthrow and are often removed or knocked down during logging operations (Thomas et al. 1979). In interior British Columbia, more than 90% of cavity nests are located in dying or dead trembling aspen, which make up only 10-15% of trees in the landscape (Martin and Eadie 1999; Martin et al. 2002).

Nest cavities are a relatively stable resource that may be used multiple times. However, few studies have examined long-term dynamics of cavity use and reuse. Sedgwick (1997) conducted the only community-based study of cavity reuse in North America, but he presented only two years of data and did not quantify the characteristics of reused cavities. Other researchers have focused on reproductive success in relation to cavity age (e.g. newly-excavated or old), particularly as influenced by predation or parasites. Nilsson et al. (1991) compared nest success of Black Woodpeckers (*Dryocopus martius*) using old and newly excavated cavities. Wiebe (2001) showed that cavity temperature was more extreme in trees in advanced stages of decay. Several researchers examined the influence of old nest material and parasites on nest-site choice and reproductive success, particularly among secondary cavity nesters using boxes (Sonerud 1985, Davis et al. 1994, Olsson and Allander 1995, Johnson 1996, Rendell and Verbeek 1996a, b). None of these studies, however, examined nest-site use in relation to characteristics of old nest cavities, or provided long-term, multi-year data on cavity use dynamics.

The Cariboo-Chilcotin region of British Columbia has one of the most diverse cavity-nesting communities in North America, with the largest proportion of woodpecker species in the province (Martin and Eadie 1999). The area near Riske Creek, BC, is comprised primarily of extensive stands of old forest and natural forest fragments in a grassland-wetland matrix. While there are some nest-box trails along roads in the area, most forest stands do not contain boxes. My study is part of a larger project on the dynamics of cavity-nesting communities in this area, which has monitored more than 1400 nests of 26 species since 1995 (Martin et al. 2002). The objectives of my study were: 1) to determine the availability and use of cavities in continuous forest and naturally-fragmented stands in the Cariboo-Chilcotin, and 2) to examine patterns of cavity reuse among guilds and species in the community.

In Chapter 2, I compare nest-site availability between continuous and fragmented forests, and examine selection of cavities at the community, guild and species levels. First, I examine the characteristics of occupied and unoccupied cavities. Then, I calculate resource selection indices (Manly et al. 1993, Krebs 1999) to determine preference for or avoidance of nest-sites at the community and species levels. I conclude that tree and habitat attributes, and nest-site context, influence cavity occupancy more than individual cavity characteristics. In Chapter 3, I address persistence of cavity use patterns across years by examining nest site reuse in a subset of previously occupied holes. I use four years of data to determine cavity reuse rates at the community, guild and species levels. I determine whether guild and species of the previous occupant influence cavity occupancy in the following year and I examine characteristics of reused cavities. Cavity reuse is defined as the use of an old (previously existing) cavity for nesting by any member of the community, not necessarily by the same individual from year to year. Chapter 4 summarizes my research results and discusses their implications for cavity nester conservation and management.

Chapter 2:
Nest-site availability and selection for a cavity-nesting community in interior British Columbia

Introduction

To understand nest-site requirements of cavity nesters, it is necessary to determine what constitutes a suitable nest-site. Many researchers have attempted to do this by reporting the characteristics of occupied cavities (e.g. Erskine and McLaren 1976, Nilsson 1984, Peterson and Gauthier 1985, and others), but it is better to estimate preference and subsequent reproductive performance directly. It is necessary to examine cavity use in relation to cavity availability across a range of conditions to determine nest-site preferences of cavity-nesters.

Nest-site selection in cavity nesting birds is influenced by a number of factors. Abundance and nesting phenology of both inter- and intraspecific competitors may influence cavity availability and selection. Competitors may prevent individuals from obtaining a cavity (Nilsson 1984, Ingold 1989, Newton 1994, Moore 1995, Loeb and Hooper 1997) or act as an indicator of potential nest-site suitability. For example, female Collared Flycatchers (*Ficedula albicollis*) use conspecific reproductive success to assess patch suitability in subsequent years (Doligez et al. 1999). Nest-site characteristics may influence predation risk and, therefore, reproductive success (Nilsson 1984, Walankiewicz 1991). For example, higher cavities may be less vulnerable to predation (Li and Martin 1991, Sachslehner 1995). Proximity to foraging habitat and food abundance may also influence nest-site selection. Nests close to abundant food resources allow adults to make more foraging trips and/or minimize time away from the nest (Eeva et al. 1989, Mallory et al. 1993). Nest-site fidelity and success in previous attempts at a site may influence nest-site use (Dow and Fredga 1984, Stanback and Dervan 2001). Finally, specific cavity attributes such as microclimate, size and cover may influence nest-site selection.

The cavity-nesting community of the Cariboo-Chilcotin region of British Columbia is one of the most diverse in North America (Martin and Eadie 1999), making up 22% of bird species in the region (Martin et al. 2002). I examine cavity use and availability for this community by:

1) calculating resource selection indices to determine nest-site preference or avoidance, and 2) examining guild- and species-specific nest-site selection patterns. In forest fragments, I compare unused cavities to those occupied by excavator and non-excavator guilds.

Methods

Study area and design

Fieldwork was conducted on Becher's Prairie, near the community of Riske Creek, in the Cariboo-Chilcotin region of BC (51° 52'N, 122°21'W; 850-1000m elevation; Figure 2.1). This area is in the Interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). It consists of native grassland interspersed with trembling aspen (*Populus tremuloides*) groves, deciduous and coniferous forest, and small lakes. The grassland was maintained historically by frequent, low intensity fires and currently by cattle grazing (BC Ministry of Forests 1995, Daigle 1996). Ninety-six percent of cavity nests in the area are in aspen (Martin and Eadie 1999). Additional details of study sites and design are given in Martin and Eadie (1999) and Wiebe (2001).

My research was conducted on 11 study sites between May-July 2000 and 2001. Five sites were large, mature, mixed forest stands (>100 ha; 80-200 yr old). The other six sites were groups of 1-20 aspen groves (0.05-3.5 ha each), 50-1000m apart. I will refer to the large forest stands as continuous forest and the groves as natural forest fragments. Continuous forests were dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), with varying amounts of lodgepole pine (*Pinus contorta* var. *latifolia*), hybrid spruce (*Picea glauca* x *engelmanni*) and aspen (Martin et al. 2002). Fragments were dominated by aspen and lodgepole pine (Martin et al. 2002). In both habitat types, trees averaged 22.0-25.0 cm in diameter at breast height (Martin et al. 2002).

Nest monitoring and data collection

In 2000, I monitored 273 old cavities, all of which were used at least once between 1995-1999, and 27 newly excavated holes. Cavities were checked for use every three days. Those within reach of a ladder (≤ 5.15 m) were inspected using flashlights and mirrors. Cavities

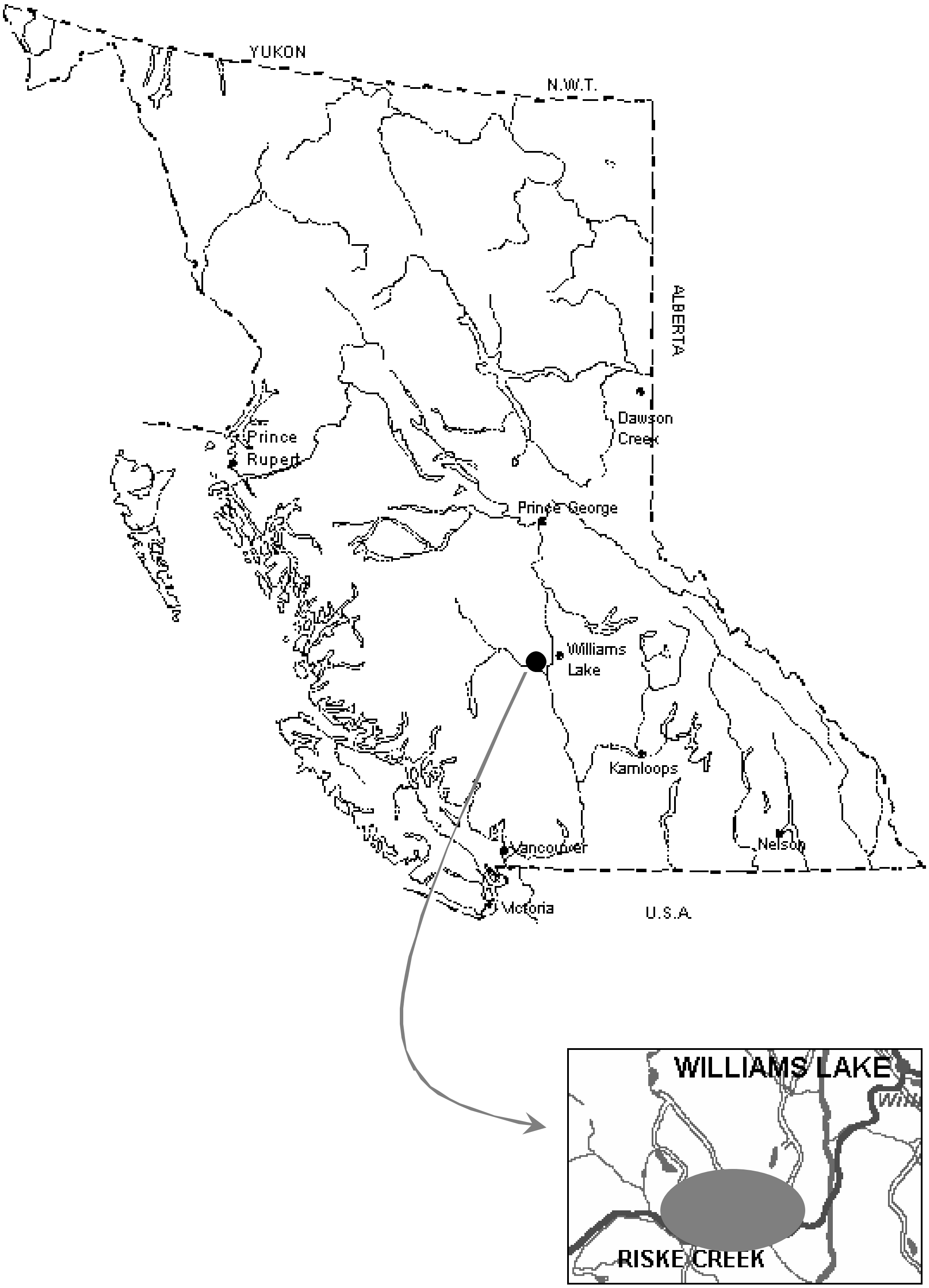

Figure 2.1. Location of Riske Creek and the study area within British Columbia, Canada.

were considered active if eggs or chicks were found. I also recorded holes used for nesting and roosting by small mammals.

In 2000, I surveyed cavity availability at each of the sites. At the five continuous sites (three with grassland edge, two with lake edge), I established three transect lines, 100 m apart, starting at the forest edge and extending 350 m into the forest. Walking along each transect, an assistant and I recorded all cavities within 10 m on either side of the line. At each of the six fragmented sites, I searched throughout the patch, beginning at the northernmost point and walking in a spiral through the patch to the centre. Total area of continuous forest surveyed was 10.5 ha (2.1 ha at each of 5 sites) and total fragment area surveyed was 24.0 ha (35 fragments, 0.05-3.0 ha).

I collected cavity, nest tree and habitat data for all active nests and unoccupied holes. Cavity variables recorded were height above ground, hole orientation (north, south, east, west), entrance area, vertical and horizontal depth, and distance to nearest cavity obstruction (e.g. branch, leaves). If a cavity had more than one entrance hole, the entrance at the lowest height was measured. Vertical cavity depth was measured from the lower lip of the entrance hole to the cavity floor. Horizontal cavity depth was measured from the inner edge of the lower lip of the entrance to the back wall of the cavity. Mode of cavity creation was categorized as excavated or natural. Excavator species was recorded if observed during excavation. Most natural cavities were located in broken branch nodes. Tree variables recorded included species (categorized as aspen or conifer), total height, diameter at breast height (DBH), and diameter at cavity height (DCH). Height to live crown (for live trees only) was measured as the height where the lowest live branch attached to the bole. Crown ratio was calculated as (tree height - height to live crown)/tree height. Cavity, tree and crown height were measured using a Suunto PM-5/1520 clinometer. Tree decay stage was recorded as healthy, unhealthy, or dead. Health was assessed using BC Ministry of Forests guidelines (Finck et al. 1989). Number of cavities in the tree was categorized as 1, 2-3 or >3. I recorded the location of each nest tree using a Garmin II-Plus or eTrex global positioning system (GPS) unit (Garmin International Inc., Olathe, KS). Habitat data recorded included distance to nearest pond or marsh and distance to nearest dry edge (grassland or road). Distances were measured either directly using 30m measuring tapes or by GPS. The area of each study site and fragment was determined using air photos for the region and ArcView GIS version 3.2 (Environmental Systems Research Institute 1999).

Between May-July 2001, I rechecked 204 cavities from the 2000 cavity surveys. Cavities and active nests were monitored as in 2000. After nesting was completed, all measurements were recorded again, except distances to nearest tree, dry edge and water as the latter were assumed to be similar across years. I did not record distance to nearest cavity obstruction in 2001. I assumed that cavity, tree, and habitat measurements for unused cavities would not change significantly between 2000-2001. Thus, only cavities occupied in 2001 were remeasured.

Data analysis

Cavities more than 5.15 m above ground (27% of cavities on my study sites; n = 301) could not be inspected and were not included in my analyses. When cavities were used twice in a breeding season, I selected randomly either the first or the second case to include in analyses. Data were analysed using SPSS for Windows version 10.0.7 (SPSS Inc. 2000). A significance level of $\alpha = 0.05$ was used. Tests were two-tailed unless otherwise indicated. Continuous variables were tested for normality using a one-sample Kolmogorov-Smirnov test at the 95% confidence level (Zar 1984).

i) Cavity density and characteristics in natural fragments versus continuous forest

Mean cavity characteristics were compared between fragmented and continuous forest in 2000 using univariate analyses. Sample sizes in continuous forest were too small to permit multivariate analyses. Independent sample *t*-tests were used for normally-distributed continuous variables (height above ground, horizontal depth, tree height, and crown ratio). Mann-Whitney *U* tests were used for non-normally distributed variables (vertical depth, entrance area, obstruction distance, DBH, DCH, distance to next tree, distance to dry edge, distance to water). Chi-square tests were used for categorical variables (orientation, tree species, decay stage, number of cavities). Where assumptions of expected values in contingency tables were not met, Fisher's Exact tests were used for categorical variables (Rosner 1982). Where sample sizes were low, decay stage was expressed as live or dead and number of cavities in tree was characterized as 1 or >1.

ii) Community-level nest-site selection - univariate and multivariate analyses

Characteristics of occupied and unoccupied cavities were compared using both univariate and multivariate analyses. Data from 2000 and 2001 were examined separately. Univariate analyses conducted were: independent sample *t*-tests for normally-distributed continuous variables, Mann-Whitney *U* tests for non-normally distributed data, and Chi-square tests or Fisher's Exact tests for categorical variables. Backward stepwise logistic regression was used to evaluate which cavity and tree variables were predictors of nest-site use (Tabachnick and Fidell 2001). Continuous variables included in the model were cavity height above ground, vertical and horizontal depth, entrance area, distance to cavity obstruction, DBH, DCH, tree height, crown ratio, distance to nearest tree, and distance to dry edge and water. Categorical variables in the model were cavity orientation, tree species, tree decay stage, and number of cavities. Variables entered the model with a significance of <0.05, and were removed at a significance of >0.10.

iii) Community-level nest-site selection – resource selection index analyses

I used Manly's selection index (Manly et al. 1993, Krebs 1999) to determine nest-site selection in relation to availability in forest fragments in 2000 and 2001. I calculated a selection coefficient and its 95% confidence interval for several nest-site variables, including habitat type (natural fragment *versus* continuous forest), cavity excavator, orientation, number of cavities in nest tree, and tree decay stage. Selection coefficients represent the proportion of a resource used in relation to the availability of that resource in the habitat. Coefficients greater than 1.0 indicate preference, while values less than 1.0 indicate avoidance. Selection coefficients were calculated as $w_i = o_i / p_i$, where w_i was the selection coefficient for cavity category i, o_i was the ratio of the number of cavities occupied in category i to the total number of cavities occupied, and p_i was the ratio of the number of cavities in category i located in the habitat to the total number of cavities. For 2000, standard errors of selection coefficients were calculated as $SE(w_i) = \sqrt{[(o_i (1 - o_i)) / Up_i]}$, where U was the total number of occupied cavities. For 2001, because a full cavity census was not conducted, standard errors were calculated as $SE(w_i) = \sqrt{[((1 - o_i) / Uo_i) + ((1 - p_i) / Mp_i)]}$, where M was the total number of cavities observed.

The Bonferroni corrected 95% confidence interval for each selection coefficient was calculated as $w_i \pm z_{a/2I}\, SE(w_i)$, where I was the number of cavity categories, and $z_{a/2I}$ was the standard normal table value corresponding to an upper tail probability of $a/2I$. Lower confidence intervals greater than 1 indicate significant selection for cavity category i, while upper confidence intervals less than 1 indicate significant avoidance of category i (Manly et al. 1993).

iv) Interguild and interspecies comparisons of nest-site use in forest fragments

Multiple comparisons tests were used to compare cavity characteristics 1) among the three guilds (PCE, WCE, SCN) and unoccupied holes, and 2) among several species and unoccupied holes. Tests used were one-way analysis of variance (ANOVA) for normally-distributed continuous variables, Kruskal-Wallis tests for non-normally distributed variables, and Chi-square tests or Fisher's Exact tests for categorical variables. Levene's test for homogeneity-of-variance was used to test the equality of variance among normally-distributed variables (SPSS Inc. 2000). Variables with significant ANOVA values were tested post-hoc with either Scheffé's test (for homogeneous variance) or Tamhane's T-2 test (for unequal variance; Kleinbaum et al. 1988, SPSS Inc. 2000). Significant Kruskal-Wallis tests were followed by pair-wise Mann-Whitney *U* tests to identify differences between pairs of guilds or species and unused cavities. Because using Mann-Whitney *U* tests for multiple comparisons may produce distorted significance levels, I used the Bonferroni correction for multiple testing (least-significant-difference method; Kleinbaum et al. 1988). *P*-values obtained from multiple comparison *U* tests were adjusted by multiplying them with a correction factor, *C*, calculated as $C = [k(k-1)]/2$, where k was the number of means or groups being compared. Corrected *P*-values are denoted by P_c. Resource selection indices were calculated for several species for cavity orientation, tree decay stage, and number of cavities in the tree in 2000 and 2001. However, due to low sample sizes, I was unable to calculate standard errors or 95% confidence intervals for resource selection coefficients for individual species. Thus, no significance levels are given for species-level selection index results.

Results

i) Cavity density and characteristics in natural fragments versus continuous forest

Cavity density ranged from 0.95 to 2.86/ha in continuous forest and 0.00 to 43.1/ha in forest fragments, with higher densities in fragments than in continuous sites ($t_{38} = 5.64$, $P < 0.001$). There were no significant differences in cavity characteristics between fragmented and continuous forest (8 variables tested, all $P > 0.05$). However, cavity trees in fragmented sites had a higher proportion of live crown relative to total tree height ($t_{102} = 6.58$, $P < 0.001$) and were farther from other trees ($U_{195} = 3911.5$, $P = 0.04$). This reflects the relative openness of forest fragment habitat. Not surprisingly, cavities in fragments were closer to grassland edge than cavities in continuous forest ($U_{217} = 4509.5$, $P = 0.006$). In continuous forest, cavities were 2-290 m from the nearest edge and number of cavities in the stand was not correlated with distance to edge ($r = 0.15$, n = 15, P = ns).

I was able to identify mode of cavity creation (excavated or naturally-occurring) for 199 cavities (Table 2.1). Primary or weak excavators created 85% of cavities, with the remaining 15% being natural holes. Fragments and continuous forest did not contain different proportions of excavated and natural cavities (Fisher's Exact test, $G = 0.39$, n = 199, $P = 0.51$). Proportions of newly-excavated and old cavities also did not differ between fragmented and continuous forest (Fisher's Exact test, $G = 2.16$, n = 166, $P = 0.60$).

ii) Community-level nest-site selection – univariate and multivariate analyses

I measured 219 cavities on survey transects in 2000, and 204 of these were checked again in 2001. Sixteen of the 204 (8%) were destroyed between 2000 and 2001, due to nest tree blowdown. Of the 188 cavities that survived to 2001 and were rechecked, 25% (n = 48) were occupied in both years, 28% (n = 52) were used in only one year and 47% (n = 88) were not used in either year. In 2000, 41% of cavities were occupied, while in 2001, 34% were occupied, but these proportions were not significantly different ($\chi^2_1 = 2.2$, $P = 0.14$). The proportions of cavities used by woodpecker, weak excavator and secondary cavity nester guilds were similar between years (Figure 2.2, Table 2.2). There were only two occupied cavities in continuous forest; all further analyses were therefore restricted to forest fragments.

Of 12 variables compared between occupied and unoccupied cavities in forest fragments in 2000 and 2001, only six differed significantly, and none were consistently significant across years (Table 2.3). Occupied cavities in forest fragments were significantly further from ponds in 2000 and closer to grassland edge in 2001. Occupied nest trees were spaced 1m further from other trees in 2000. Occupied cavities were lower on the tree, and had larger internal volume and larger entrances than unused cavities in 2001. Using logistic regression, cavity use in forest fragments was best predicted by vertical and horizontal depth, number of cavities in the tree, and distance to next nearest tree (Table 2.4).

iii) Community-level nest-site selection – resource selection index analyses

Of seven variables examined using resource selection indices in 2000 and 2001, two (habitat type and number of cavities in the nest tree) were significantly preferred or avoided (Table 2.5). Other variables examined included tree species, tree health, excavator, cavity age, and cavity orientation. Only 9-10% of cavities in continuous forest were occupied in either 2000 or 2001, while 35-44% of cavities in natural fragments were used. Cavities in continuous forest were avoided, while those in fragments were used in proportion to their availability (Figure 2.3, Table 2.5).

Despite strong selection for aspen at Riske Creek (Martin and Eadie 1999), existing cavities in aspen were used in proportion to their availability (Table 2.5). Cavities in live, unhealthy trees were preferred for nesting, while cavities in dead trees were avoided, but this was not significant (Table 2.5). Only one cavity was located in a live, healthy tree, and this was occupied in both 2000 and 2001.

When cavities created by woodpeckers and weak excavators were pooled, the proportions of excavated and natural cavities occupied did not differ in either year (2000: $\chi^2_1 = 0.02$, $P = 0.88$; 2001: $\chi^2_1 = 0.44$, $P = 0.51$). When I examined individual excavator species, Red-naped Sapsucker and natural cavities were avoided and Northern Flicker cavities were preferred, but this was not significant (Figure 2.4, Table 2.5). However, the proportion of Northern Flicker cavities occupied (50-56%) was greater than that of Red-naped Sapsucker cavities (17-29%; 2000: $\chi^2_1 = 5.52$, $P = 0.02$; 2001: $\chi^2_1 = 7.87$, $P = 0.005$).

Where cavity age (newly-excavated or old) could be determined (n = 155), 10% of cavities were newly-excavated and 90% were old in 2000 (data were not available on newly-excavated cavities in 2001). Seventy-three percent of new cavities were occupied in 2000

Table 2.1. Number of excavated and natural cavities in forest fragments (6 sites; 24 ha total) and in continuous forest (5 sites; 10.5 ha total) at Riske Creek, BC in 2000.

	Forest fragments		**Continuous forest**		**Total**	
Excavator species	**n**	**%**	**n**	**%**	**n**	**%**
Primary excavators						
Northern Flicker	89	49.7	-	-	89	44.7
Red-naped Sapsucker	24	13.4	-	-	24	12.1
Hairy Woodpecker	2	1.1	2	10.0	4	2.0
Downy Woodpecker	1	0.6	-	-	1	0.5
Pileated Woodpecker	-	-	1	5.0	1	0.5
Unidentified woodpecker	35	19.6	13	65.0	48	24.1
Total woodpeckers	*151*	*84.4*	*16*	*80.0*	*167*	*83.9*
Weak excavators						
Red-breasted Nuthatch	1	0.6	-	-	1	0.5
Black-capped Chickadee	1	0.6	-	-	1	0.5
Total weak excavators	*2*	*1.1*	-	-	*2*	*1.0*
Natural	26	14.5	4	20.0	30	15.1
Total	**179**	**89.9**	**20**	**10.1**	**199**	**100.0**

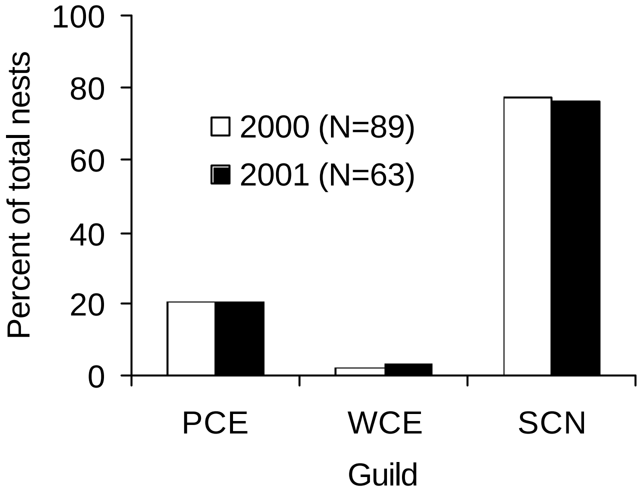

Figure 2.2. Proportion of total nests occupied by primary cavity excavators (PCE), weak cavity excavators (WCE) and secondary cavity nesters (SCN) at Riske Creek, BC, in 2000 and 2001 ($\chi^2_2 = 0.13$, $P = 0.94$).

Table 2.2. Nests of cavity-nesting birds and mammals on study sites near Riske Creek, BC in 2000 and 2001.

		2000		2001	
Species	**Code**	**n**	**% of total nests (N = 89)**	**n**	**% of total nests (N = 63)**
Primary excavators					
Northern Flicker *Colaptes auratus*	NOFL	15	16.9	13	20.6
Red-naped Sapsucker *Sphyrapicus nuchalis*	RNSA	3	3.4	0	-
Total woodpeckers		*18*	*20.2*	*13*	*20.6*
Weak excavators					
Red-breasted Nuthatch *Sitta canadensis*	RBNU	2	2.2	2	3.2
Total weak excavators		*2*	*2.2*	*2*	*3.2*
Secondary cavity nesters					
American Kestrel *Falco sparverius*	AMKE	2	2.2	1	1.6
Bufflehead *Bucephala albeola*	BUFF	2	2.2	2	3.2
European Starling *Sturnus vulgaris*	EUST	25	28.1	20	31.7
Mountain Bluebird *Sialia currucoides*	MOBL	9	10.1	9	14.3
Mountain Chickadee *Poecile gambeli*	MOCH	7	7.9	4	6.3
Tree Swallow *Tachycineta bicolor*	TRES	13	14.6	10	15.9
Unidentified SCN bird[a]		0	-	1	1.6
Red Squirrel *Tamiasciurus hudsonicus*	TAHU	7	7.9	1	1.6
Unidentified small mammal		4	4.5	0	-
Total secondary cavity nesters		*69*	*77.5*	*48*	*76.2*

[a] Mountain Bluebird or European Starling; eggs in cavity, adult never observed

Table 2.3. Characteristics of occupied and unoccupied cavities (mean ± standard error) in two years at Riske Creek, BC, with results of univariate *t*-tests and Mann-Whitney *U* tests. See text for results of logistic regression.

	2000				**2001**			
	Occupied	**Not occupied**			**Occupied**	**Not occupied**		
Characteristics	Mean ± SE (n)[a]	Mean ± SE (n)	*Test statistic*[b]	*P*	Mean ± SE (n)	Mean ± SE (n)	*Test statistic*[b]	*P*
Cavity height (m)	2.6 ± 0.12 (87)	2.8 ± 0.12 (110)	-1.34	0.18	2.4 ± 0.12 (62)	2.8 ± 0.12 (116)	-2.85	**0.005**
Vertical depth (cm)	26.0 ± 2.62 (79)	27.5 ± 2.97 (82)	3140.5	0.74	27.4 ± 2.31 (53)	27.4 ± 2.94 (92)	1988.5	0.07
Horizontal depth (cm)	13.8 ± 0.60 (82)	12.6 ± 0.51 (87)	1.56	0.12	16.5 ± 0.77 (61)	12.6 ± 0.51 (97)	4.44	**< 0.001**
Entrance area (cm^2)	27.1 ± 1.69 (82)	26.6 ± 2.22 (86)	3188.5	0.28	30.5 ± 1.83 (62)	26.6 ± 2.07 (96)	2211.5	**0.006**
DBH (cm)	34.2 ± 1.13 (87)	32.0 ± 0.99 (109)	4222.5	0.19	34.2 ± 1.30 (62)	31.7 ± 0.79 (116)	1.65[c]	0.10
DCH (cm)	32.0 ± 1.12 (83)	30.7 ± 1.31 (84)	0.75	0.46	32.0 ± 1.20 (62)	29.7 ± 0.90 (96)	1.58	0.12
Tree height (m)	10.0 ± 0.48 (87)	9.0 ± 0.43 (109)	1.48	0.14	9.3 ± 0.54 (62)	9.2 ± 0.41 (116)	0.11	0.91
Crown ratio	0.5 ± 0.02 (51)	0.6 ± 0.02 (44)	-0.90	0.37	0.6 ± 0.03 (35)	0.6 ± 0.02 (55)	0.35	0.73
Obstruction distance (m)	2.6 ± 0.30 (74)	2.7 ± 0.30 (93)	3283.0	0.61	3.0 ± 0.40 (52)	2.5 ± 0.27 (105)	2279.0	0.09
Next tree distance (m)	2.8 ± 0.62 (80)	2.0 ± 0.16 (95)	3145.0	**0.05**	3.1 ± 0.84 (58)	2.0 ± 0.16 (109)	2643.5	0.08
Dry edge distance (m)	13.6 ± 1.12 (87)	15.2 ± 1.01 (110)	-1.07	0.29	10.9 ± 1.11 (62)	15.5 ± 1.04 (116)	2695.0[d]	**0.006**
Water distance (m)	213.9 ± 26.45 (86)	163.0 ± 23.8 (107)	3817.5	**0.04**	244.7 ± 32.7 (62)	191.0 ± 24.5 (116)	3091.5	0.12

[a] n = number of cavities

[b] Except where indicated, test statistic used was:

t: Cavity height, horizontal depth, DCH, tree height, crown ratio, dry edge distance

U: Vertical depth, entrance area, DBH, obstruction distance, next tree distance, water distance

[c] *t* test used in 2001

[d] *U* test used in 2001

Table 2.4. Variables associated with cavity use in forest fragments in 2000 and 2001 (backward step-wise logistic regression).

Variable[a]	2000 -2 Log Likelihood	df	*P*	2001 -2 Log Likelihood	df	*P*
Vertical depth (cm)	4.1	1	0.04	-	-	-
Horizontal depth (cm)	-	-	-	14.1	1	<0.001
No. cavities in tree (1, 2-3, >3)	7.9	2	0.02	5.6	2	0.06
Distance to next tree (m)	4.5	1	0.03	4.9	1	0.03

[a] Vertical depth entered model in 2000, horizontal depth entered model in 2001.

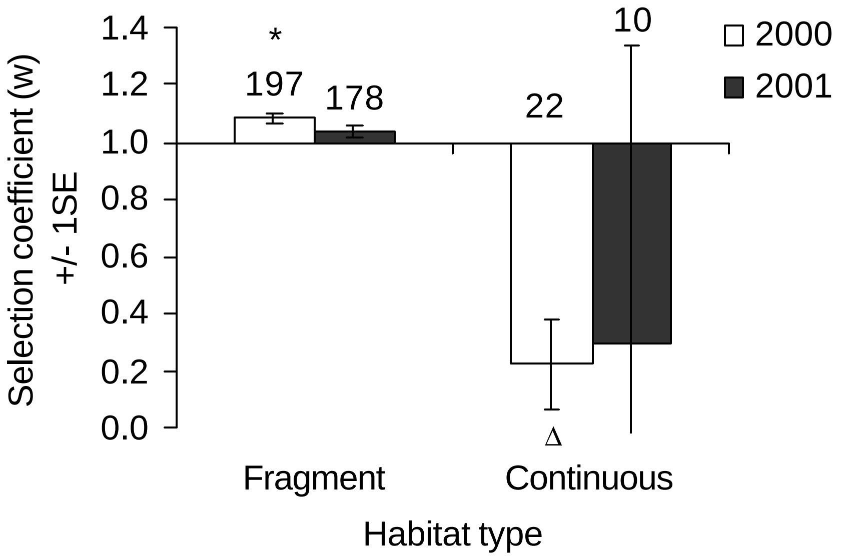

Figure 2.3. Cavity selection in natural fragments and continuous forest in 2000 and 2001. Selection coefficient *w* is proportion of cavities used/available. *w* >1 implies selection, *w* <1 implies avoidance (* indicates significant preference, $^{\Delta}$ indicates significant avoidance of cavities based on the 95% confidence interval of *w* for each habitat type; see text and Table 2.5).

Table 2.5. Cavity selection coefficients[a] (95% confidence interval) for cavity use in 2000 and 2001. All (except habitat type) are for forest fragments only.

Cavity characteristic	**2000**	**2001**
1) Habitat type		
Natural fragment	1.09* (1.05-1.13)	1.04 (0.99-1.09)
Continuous	0.22* (-0.13-0.57)	0.30 (-2.03-2.63)
2) Tree species		
Aspen	1.01 (0.95-1.06)	0.97 (0.88-1.07)
Conifer	0.91 (-0.09-1.90)	1.44 (0.25-2.62)
3) Decay stage		
Healthy	2.26 (-3.11-7.65)	2.87 (-0.49-6.23)
Unhealthy	1.19 (0.93-1.45)	1.12 (0.89-1.35)
Dead	0.80 (0.55-1.05)	0.74 (0.17-1.31)
4) Excavator		
Northern Flicker	1.08 (0.85-1.31)	1.26 (0.98-1.48)
Red-naped Sapsucker	0.56 (0.06-1.07)	0.44 (-0.87-1.72)
Other excavator species	1.48 (0.39-2.57)	0.76 (-0.63-2.73)
Natural	0.89 (0.30-1.48)	0.75 (-0.28-1.72)
5) Cavity age		
Newly-excavated	1.50 (0.56-2.43)	N/a
Old	0.95 (0.85-1.05)	N/a
6) Number of cavities in tree		
1	1.43* (1.12-1.75)	1.36* (1.03-1.69)
2-3	0.84 (0.56-1.13)	0.86 (0.43-1.29)
>3	0.35* (-0.01-0.72)	0.26 (-1.47 – 1.99)
7) Orientation		
North	0.81 (0.29-1.32)	0.90 (0.12-1.68)
East	0.76 (0.28-1.25)	1.18 (0.48-1.88)
South	1.25 (0.81-1.69)	1.05 (0.47-1.64)
West	1.03 (0.64-1.42)	0.91 (0.36-1.45)

[a] Coefficients represent the ratio of cavity use to availability. * 95% confidence intervals not containing 1indicate significant selection (>1) or avoidance (<1).

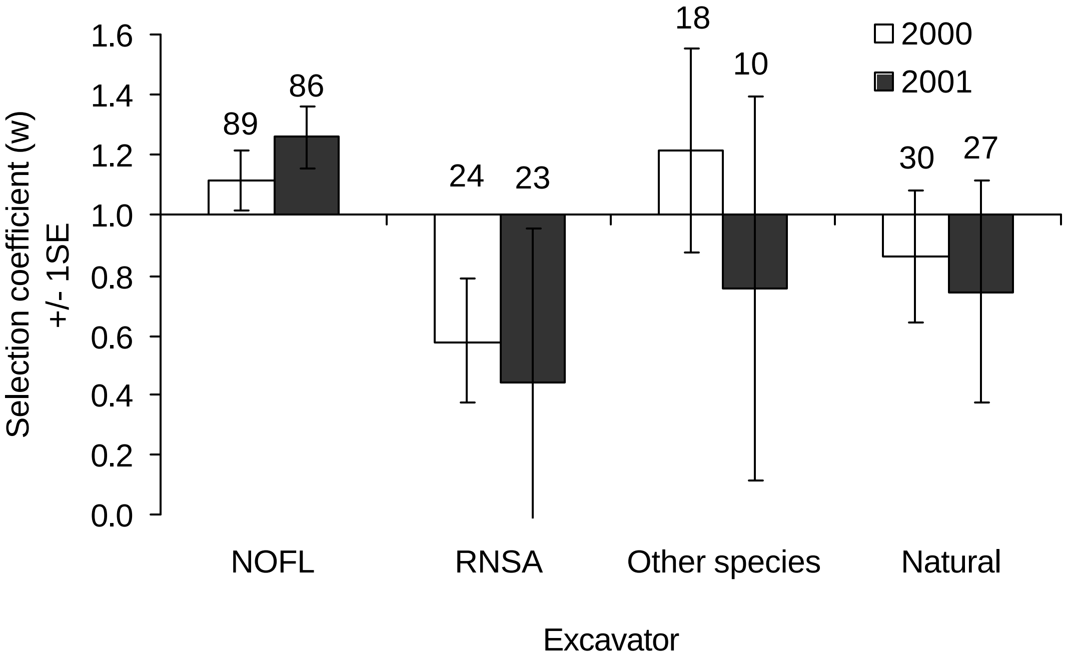

Figure 2.4. Selection of cavities excavated by Northern Flickers (NOFL), Red-naped Sapsuckers (RNSA), other excavator species, and naturally-occurring holes in forest fragments in 2000 and 2001 (see text and Table 2.5).

compared to 46% of old cavities ($\chi^2_1 = 3.9$, $P = 0.05$). Newly-excavated cavities were used more than predicted from their availability, while old cavities were used in proportion to their availability but this was not significant (Table 2.5). Not surprisingly, when examined by guild, SCNs used significantly fewer newly-excavated cavities than did PCEs (Figure 2.5). WCEs could not be included in this analysis because of low sample sizes.

Cavity-nesters selected nest-sites on the basis on total number of cavities in the tree. In both years, trees with only one cavity were preferred while trees with more than 3 cavities were avoided (Figure 2.6, Table 2.5). Trees with 2-3 cavities were used in proportion to their availability. There was no selection on the basis of cavity orientation (Table 2.5). While north-facing cavities were avoided in both years, this was not significant.

iv) Interguild and interspecies comparisons of nest-site use in forest fragments

Of twelve variables compared across guilds in 2000 and 2001, vertical and horizontal depth and DBH differed by guild in both years. Cavity height above ground, entrance area and distance to dry edge differed by guild in 2001 only (Table 2.6). PCE nest cavities were deeper than SCN cavities (2000: $U_{75} = 115.0$, $P_c = 0.006$; 2001: $U_{50} = 33.5$, $P_c = 0.006$) and unused cavities (2000: $U_{96} = 305.0$, $P_c = 0.006$; 2001: $U_{103} = 237.5$, $P_c = 0.006$). They were also lower on the tree than SCN cavities (Tamhane's T2 Post-hoc test: n = 60, $P = 0.008$) and unused cavities (Tamhane's test: n = 129, $P < 0.001$). PCE cavities were larger internally than SCN cavities (Scheffe's Post-hoc test: n = 59, $P = 0.02$). PCE cavities had larger entrances than unused cavities ($U_{107} = 296.0$, $P_c = 0.01$), and SCN cavities had larger entrances than WCE cavities ($U_{47} = 2.0$, $P_c = 0.04$). PCEs and SCNs did not differ in the proportions of live or dead nest trees used (2000: $\chi^2_1 = 0.30$, $P = 0.58$; 2001: $\chi^2_1 = 0.01$, $P = 0.94$), or in the number of other cavities in the nest tree (two categories: 1, >1; 2000: $\chi^2_1 = 0.97$, $P = 0.33$; 2001: $\chi^2_1 = 0.51$, $P = 0.48$). WCE nests in both years were in unhealthy trees, but 2000 nest trees had only one cavity, while in 2001 they each had 2-3 cavities. Diameter at cavity height, tree height, crown ratio, distance to cavity obstruction (e.g. branch, leaves), distance to next adjacent tree and distance to water did not differ among guilds in either year.

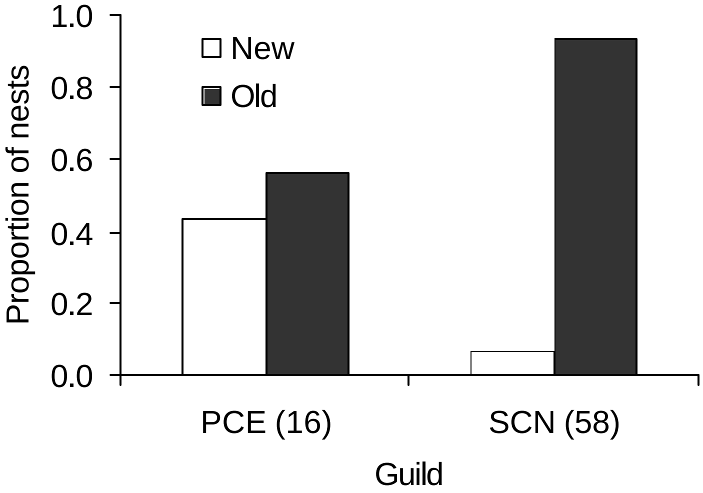

Figure 2.5. Proportions of newly-excavated versus old cavities used for nesting by woodpeckers (PCE) and secondary cavity nesters (SCN) in natural forest fragments (Fisher's Exact test, *G* = 11.2, n = 74, *P* = 0.001)

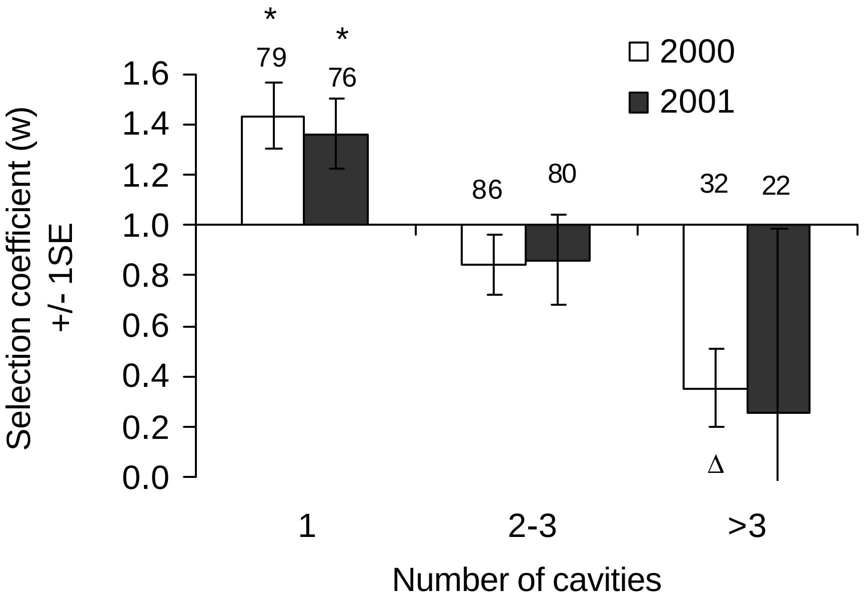

Figure 2.6. Nest-site selection in relation to number of holes in tree in forest fragments in 2000 and 2001 (* indicates significant preference, $^{\Delta}$ indicates significant avoidance based on the 95% confidence interval of *w* for each cavity type; see text and Table 2.5).

Table 2.6. Mean nest-site characteristics of three cavity-nesting guilds in forest fragments near Riske Creek, BC in 2000 (this page) and 2001 (next page).

a) 2000:

	Primary cavity excavators			Weak cavity excavators			Secondary cavity nesters			Unused		
Characteristic[a]	Mean[b]	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Cav. ht (m)	2.3	0.24	18	2.1	0.64	2	2.7	0.14	67	2.8	0.12	110
Vert. dep. (cm) **	47.6**a**	7.49	16	10.0**ab**	0.55	2	20.8**b**	2.30	61	27.5**b**	2.97	82
Hor. dep. (cm) *	15.4**a**	1.46	17	6.8**a**	2.25	2	13.6**a**	0.65	63	12.6**a**	0.51	87
Ent. area (cm^2)	28.3	2.35	16	10.7	2.47	2	27.3	2.06	64	26.6	2.22	86
DBH (cm) *	37.3**a**	2.59	18	20.4**a**	0.65	2	33.8**a**	1.26	67	32.0**a**	0.99	109
DCH (cm)	33.8	2.11	17	19.2	2.50	2	32.0	1.31	64	30.7	1.31	84
Tree ht (m)	9.5	1.23	18	10.2	1.00	2	10.1	0.53	67	9.0	0.43	109
Crown ratio	0.5	0.06	10	N/a	N/a	0	0.6	0.03	41	0.6	0.02	44
Obst. dist. (m)	2.8	0.78	13	4.2	1.75	2	2.6	0.34	41	2.7	0.30	93
Next tree (m)	2.9	0.61	16	1.3	1.00	2	2.9	0.79	59	2.0	0.16	95
Dry edge dist (m)	13.4	3.24	18	17.8	4.25	2	13.5	1.18	67	15.2	1.01	110
Water dist (m)	255.7	61.4	18	320.0	320.0	2	199.3	29.3	66	163.0	23.8	107

[a] ANOVA or Kruskal-Wallis tests used to detect differences across 3 guilds and unused; * $P < 0.05$, ** $P < 0.01$

[b] Values sharing the same letter within rows do not differ significantly (Scheffe's, Tamhane's T-2, or Bonferroni-corrected Mann-Whitney *U* post-hoc tests, $P > 0.05$).

Table 2.6 cont. Mean nest-site characteristics of three cavity-nesting guilds in forest fragments near Riske Creek, BC in 2000 (previous page) and 2001 (this page).

b) 2001:

	Primary cavity excavators			Weak cavity excavators			Secondary cavity nesters			Unused		
Characteristic[a]	Mean[b]	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
b) 2001:												
Cav ht (m) **	1.7**a**	0.18	13	2.0**ab**	0.71	2	2.5**b**	0.14	47	2.8**b**	0.12	116
Vert. dep. (cm) **	43.8**a**	3.31	13	11.5**ab**	-	1	22.4**b**	2.37	39	27.4**b**	2.94	92
Hor. dep (cm) **	16.1**ab**	0.89	13	6.3**ab**	1.30	2	17.1**a**	0.94	46	12.6**b**	0.51	97
Ent. area (cm^2) **	35.7**abc**	2.45	13	8.6**ac**	0.82	2	30.0**b**	2.20	47	26.6**bc**	2.07	96
DBH (cm) *	37.1**a**	2.57	13	19.7**a**	1.30	2	34.0**a**	1.50	47	31.7**a**	0.79	116
DCH (cm)	33.8	2.02	13	20.0	2.05	2	32.0	1.44	47	29.7	0.90	96
Tree ht (m)	8.0	1.34	13	7.2	0.25	2	9.7	0.60	47	9.2	0.41	116
Crown ratio	0.6	0.05	7	N/a	N/a	0	0.5	0.03	28	0.6	0.02	55
Obst. dist (m)	2.8	0.98	10	6.0	-	1	2.9	0.45	41	2.5	0.27	105
Next tree (m)	2.4	0.36	12	1.4	0.85	2	3.3	1.10	44	2.0	0.16	109
Dry edge dist (m) *	9.2**a**	1.94	13	6.8**a**	6.75	2	11.5**a**	1.33	47	15.5**a**	1.04	116
Water dist (m)	182.8	59.3	13	320.0	320.0	2	258.6	38.7	47	191.0	24.5	116

[a] ANOVA or Kruskal-Wallis tests used to detect differences across 3 guilds and unused; * $P < 0.05$, ** $P < 0.01$

[b] Values sharing the same letter within rows do not differ significantly (Scheffe's, Tamhane's T-2, or Bonferroni-corrected Mann-Whitney *U* post-hoc tests, $P > 0.05$).

I had sufficient sample sizes ($n \geq 5$) to compare nest-sites used by Northern Flicker, Mountain Bluebird, Tree Swallow and European Starling in both years, and also Mountain Chickadee and Red Squirrel in 2000. Mean nest site characteristics of each species are summarized in Appendix I. Of twelve variables examined, only four (vertical and horizontal depth, entrance area, and DCH) differed among species in both years. Variables with significant pair-wise differences in both years (vertical and horizontal depth, entrance area) are summarized in Figure 2.7. Only vertical depth varied consistently among species in both years; Northern Flicker cavities were deeper than those of all other species except Red Squirrels and were deeper than unused holes (Figure 2.7).

In both years, there was considerable variation in orientation of occupied cavities (Figure 2.8). Only Mountain Bluebirds consistently avoided south-facing cavities. There was less variation in nest-site selection in relation to tree decay stage, with Northern Flickers, Mountain Bluebirds and Red Squirrels using live and dead trees in proportion to their availability (Figure 2.9). Tree Swallows, European Starlings and Mountain Chickadees, however, preferred live, unhealthy trees and avoided dead trees. In both years, Northern Flickers, Tree Swallows and European Starlings selected trees with only one cavity and avoided those with more than one hole (Figure 2.10).

Discussion

To determine nest-site requirements of cavity nesters, it is necessary to examine nest-site use in relation to availability. Because secondary cavity nesters, in particular, cannot create their own nest holes, they may be constrained by nest-site preferences of excavators. However, few studies have examined use and availability of natural nest cavities at the community level in unharvested landscapes. My study addressed this by determining nest-site availability for a diverse community of cavity nesters in mature mixed forests and aspen groves of the Cariboo-Chilcotin, British Columbia. By calculating resource selection indices, I was able to determine community, guild and species nest-site preferences.

Cavity density and use in natural fragments versus continuous forest

Overall cavity occupancy rates of 33-41% at Riske Creek were generally lower than those reported in other studies. Peterson and Gauthier (1985) found 57% of cavities used in aspen

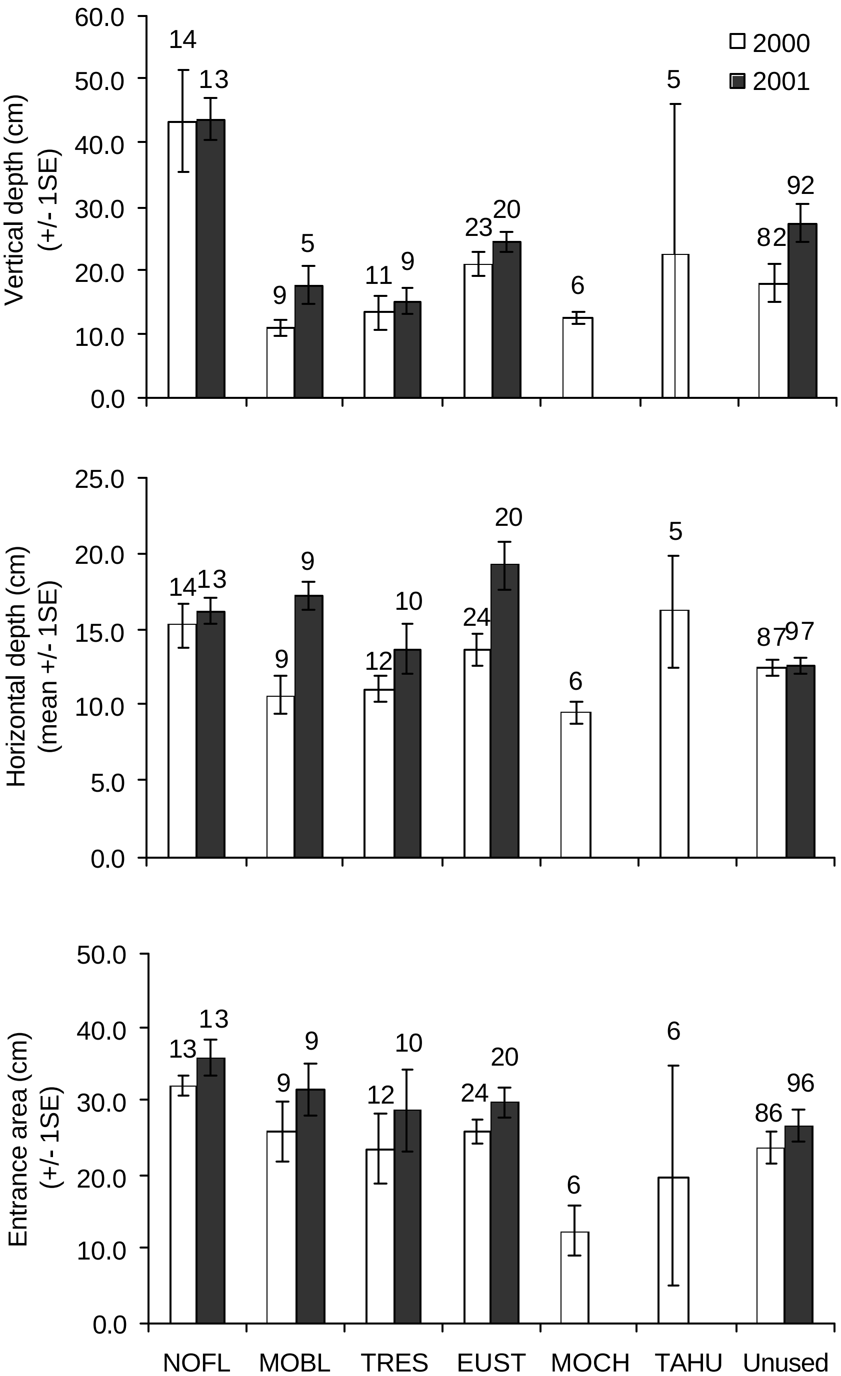

Figure 2.7. Nest-site characteristics of several cavity-nesting species near Riske Creek, BC, in 2000 and 2001. Variables presented had significant pair-wise differences in multiple comparison tests in both years (see Appendix I for details and results of post-hoc tests).

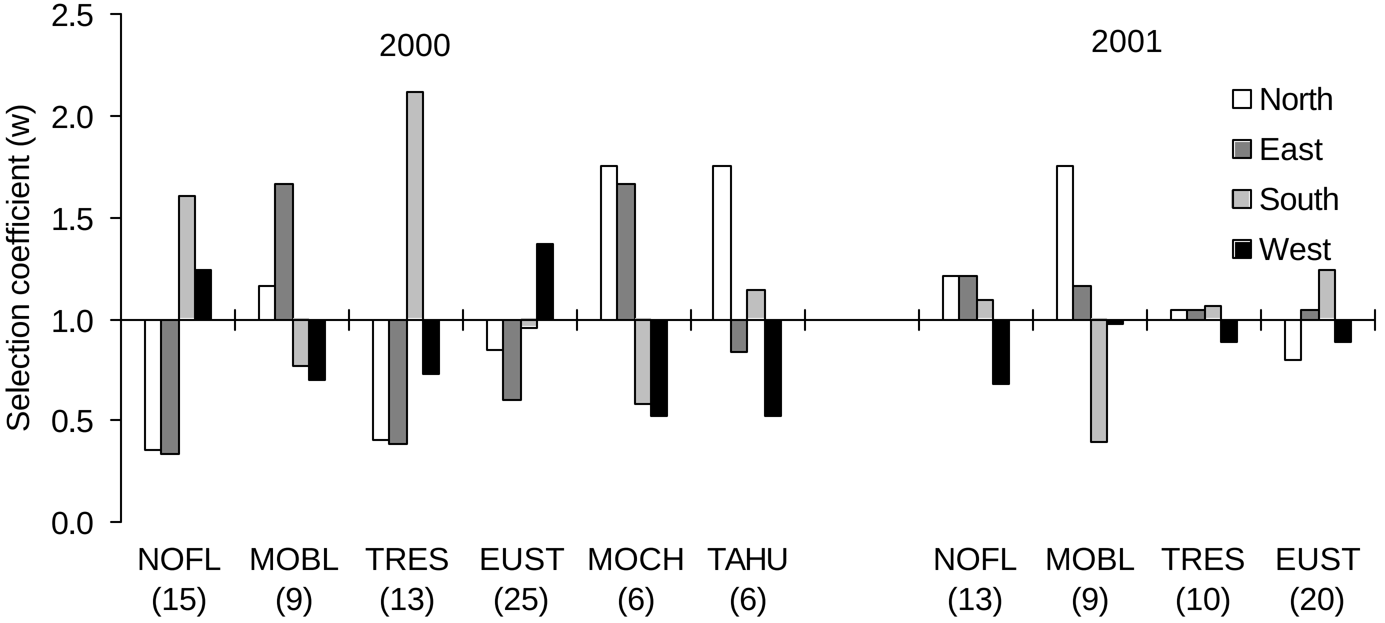

Figure 2.8. Nest-site selection by cavity nesters in relation to hole orientation in forest fragments in 2000 and 2001. See Table 2.2 for species codes.

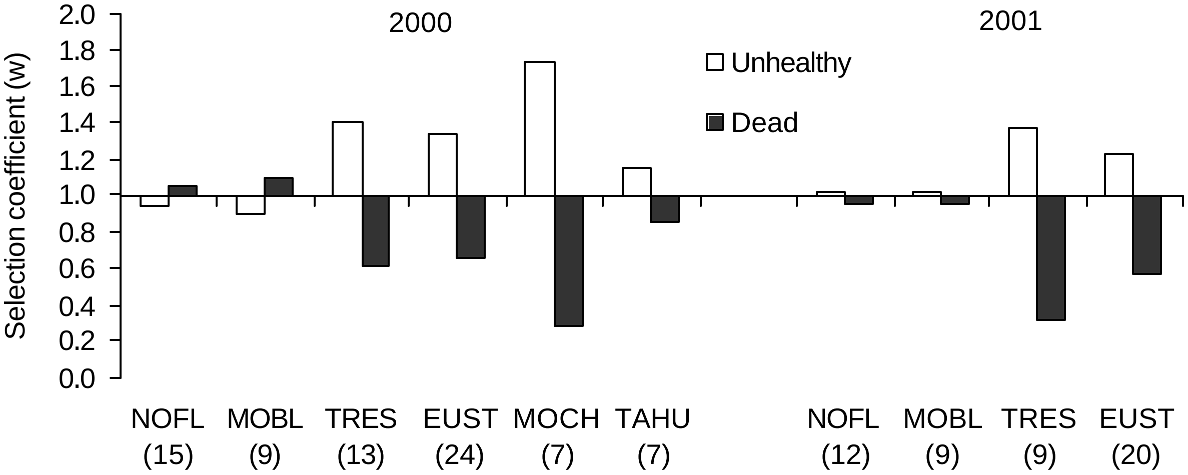

Figure 2.9. Nest-site selection by cavity nesters in relation to tree health in forest fragments in 2000 and 2001.

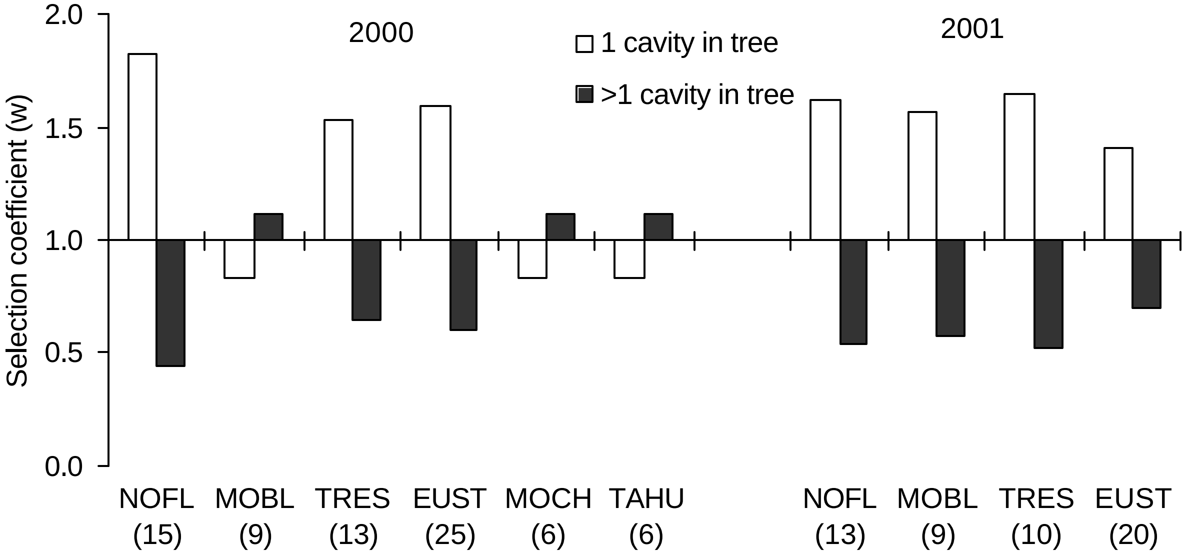

Figure 2.10. Nest-site selection by cavity nesters in relation to number of cavities in the nest tree, in forest fragments in 2000 and 2001.

parkland habitat in the same region. Occupancy rates of 9% in continuous forest at Riske Creek were lower than 20% observed in interior boreal forests in Sweden (Johnsson et al. 1993) and 35-74% in deciduous forests in Arizona and Michigan (Boyer 1975, Brush 1983). The woodpecker assemblage at Riske Creek is diverse (Martin and Eadie 1999), providing a variety of options for other cavity users. Northern Flickers, in particular, may produce a surplus of cavities, resulting in low overall occupancy rates. Nest-site competition is negatively related to nest-site abundance (Lindell 1996). Therefore, the influence of cavity creation and loss on nest-site availability and competition needs to be examined.

At the community level, cavity-nesters in the Cariboo-Chilcotin preferred cavities in forest fragments to those in continuous forest. However, there were no differences in cavity characteristics between the two habitats. Thus, nest-site context such as proximity to foraging habitat is probably a greater influence on cavity occupancy in continuous forest than is cavity quality. This may represent the preferences of the most abundant cavity nesters in the region, Northern Flickers, European Starlings, Mountain Bluebirds and Tree Swallows, all of which are associated with open habitat (Robertson et al. 1992, Cabe 1993, Moore 1995, Power and Lombardo 1996). Nests in fragments may provide better foraging opportunities for those species, which forage either aerially (Tree Swallows, Mountain Bluebirds) or in grassland (Northern Flickers, European Starlings).

Forest fragments may offer reduced predation rates. The large proportion of unoccupied cavities in forest fragments (56% in 2000, 65% in 2001) may increase search time required for predators to locate occupied holes (Martin and Roper 1988). Nests with clumped distribution may have lower predation rates (Richardson and Knapton 1993) because the number of vigilant individuals is increased (Brown and Brown 1987, Soler and Soler 1996). Additionally, nest predation rates in forest fragments may be lower than in continuous forest because of reduced abundance of mammalian predators (Tewksbury et al. 1998). Little is known about predation pressures for cavity nesters at Riske Creek. Further research is needed to determine if predation rates differ between natural fragments and continuous forests in this region, which would help to explain the preference for forest fragments by some species in this community.

Nest-site selection - community, guild and species comparisons

While cavity density was higher in forest fragments than in continuous forest, within fragments cavity nesters preferred trees with only one cavity. Cavity nesters may mitigate the costs of nesting at high densities, such as increased competition, by selecting trees with fewer holes. Tree Swallows, for example, space nests as far apart as possible when cavities are clumped (Robertson et al. 1992). The number of cavities in a tree may be correlated with tree decay stage and health, and be an indicator of tree age and stability. Trees with multiple cavities may have extensive heartrot and be susceptible to blowdown.

The proportion of cavities created by Northern Flickers (45%) was similar to 50% observed in eastern British Columbia (Holt and Martin 1997). Cavities created by Northern Flickers at Riske Creek were selected for nesting by other species more than predicted from their availability, while Red-naped Sapsucker cavities were avoided. This may be due to the larger size of Northern Flicker cavities, which can accommodate a broader range of secondary cavity nesting species. Peterson and Gauthier (1985) found that cavity volume and entrance size were the most important variables in determining cavity occupancy. Larger cavities may accommodate larger clutch sizes (Rendell and Verbeek 1996a, Stewart and Robertson 1999). They may also provide better heat dissipation on hot days (Van Balen 1984, Alatalo et al. 1988), and reduce competition for space and feeding positions among siblings (Slagsvold 1989). Because larger cavities can accommodate more cavity-nesting species, competition for these holes may be more intense than for smaller cavities. Northern Flickers and starlings compete aggressively for cavities and often usurp or destroy each other’s nests (Moore 1995, K. Martin and K.L. Wiebe unpubl. data). Given the importance of flickers as cavity excavators, the impact of increased starling abundance on their populations in the last 30 years in the region (Peterson and Gauthier 1985, Campbell 1997) needs to be established.

Newly-excavated cavities were preferred to old cavities for nesting, and both excavator and non-excavator species used new cavities. Both new and old cavities have potential advantages and disadvantages for cavity nesters. Old cavities may be more susceptible to predation as predators learn the location of nest sites (Sonerud 1985, 1989, 1993, Nilsson et al. 1991) and they may contain nest parasites or debris (Rendell and Verbeek 1996a). However, some cavity nesters prefer cavities or nest boxes with old nesting material (Davis et al. 1994, Mappes et al. 1994, Olsson and Allander 1995). Old material may be an indicator of nest-site suitability and potential nesting success (Nilsson 1984, Finch 1989). Returning cavity nesters may have less information on the suitability of a new cavity than one they observed or nested in the previous year. Reproductive success of woodpeckers and secondary cavity nesters is higher in new cavities at Riske Creek (K.E.H. Aitken and K. Martin, unpubl. data) but competition for these sites may be intense. The use of old cavities may be an adaptation to avoid aggression and interference between cavity nesting species (Brush 1983). Chapter 3 and Aitken et al. (2002) provide extended discussions of nest cavity reuse.

Cavity orientation varied among species and there was no selection at the community level for a particular aspect. This agrees with several other studies of nest-site selection in cavity and cup nesters, in which orientation varied with species and habitat (Rohrbaugh and Yahner 1997, Zwartjes and Nordell 1998, Nelson and Martin 1999). Tree Swallows and American Kestrels prefer south- or southeast-facing cavities or boxes (Rendell and Robertson 1994, Rohrbaugh and Yahner 1997). Dobkin et al. (1991) found that excavators preferred east-facing cavities, while non-excavators showed no preference. Other researchers have found no relationship between nest-site selection and orientation in Red-naped Sapsuckers (McClelland and McClelland 2000) and Collared Flycatchers (*Ficedula albicollis*; Sachslehner 1995). In general, east- or south-facing nests may have thermal advantages such as reduced heat loss and enhanced development rates of eggs and nestlings (Dobkin et al. 1991). However, there was no relationship between cavity microclimate and reproductive success in Northern Flickers in this study area (Wiebe 2001). In open habitats in the northern hemisphere, such as grasslands or deserts, nests oriented toward the north or northeast may maximize the amount of light received in the morning, while being shaded from the sun during the hottest part of the day (Nelson and Martin 1999). For cavity-nesters in forests, however, orientation may depend on the openness of the habitat, location of canopy gaps, and even decay stage of the nest tree (Wiebe 2001). Orientation selection may also be constrained by cavity availability and competition, as well as by surrounding habitat characteristics such as streams or ponds, woodland edge, and nearby obstructions.

Red-breasted Nuthatches and Black-capped Chickadees were common on my study sites (Martin and Eadie 1999) but these weak excavators were underrepresented in my cavity use data. This may be because the area surveyed was not large enough to encompass more than a few of their territories. Both species have larger territories than the most common secondary cavity nesters on my study sites. While nuthatches and Black-capped Chickadees defend nest territories up to five hectares (Smith 1993, Ghalambor and Martin 1999), Tree Swallows and European Starlings defend only the immediate area around the nest cavity (Robertson et al. 1992, Cabe 1993, Power and Lombardo 1996). Northern Flickers also maintain territorial boundaries only a small distance from the nest tree (Moore 1995, Elchuk 2001, K.L. Wiebe unpubl. data). Because nuthatches and chickadees are bark and foliage gleaners (Smith 1993, Ghalambor and Martin 1999), they may require larger stands of mixed forest than grassland or aerial foragers. Finally, nuthatch territory abundance is influenced by snag density (Ghalambor and Martin 1999). Forest fragments at Riske Creek may not provide adequate numbers of dead trees for nesting, limiting the abundance of nuthatches in small patches. Weak excavators at Riske Creek are negatively associated with degree of fragmentation (Martin and Eadie 1999), suggesting they either prefer interior habitat or are unable to compete with larger cavity nesters in open habitats. A more complete survey of weak excavator nest sites at Riske Creek would help determine the role this guild plays in nest web structure and function.

Red Squirrels are abundant in my study area (K. Martin, unpubl. data) and both compete with and prey on other cavity nesting species. However, while I recorded nest and roost cavities of squirrels, I did not examine interactions between squirrels and other cavity nesters. Red squirrels use cavities throughout the winter as roosts and food caches. This may influence the likelihood a cavity is occupied by other cavity nesters during the breeding season. As well, the presence of a squirrel nest may affect whether other species use cavities in the vicinity. This is an important relationship that needs to be examined.

Summary

Nest-site selection by cavity nesters at Riske Creek was influenced primarily by tree and habitat attributes. Thus, nest-site quality may be determined by context, such as proximity to foraging sites, rather than by cavity characteristics. While forest fragments were preferred for nesting, it is important to note that these habitats were characterized by long-term, natural edges adjacent to native grassland. While multi-tree reserves in harvested landscapes may mitigate some of the effects of forest cutting (Schieck and Hobson 2000), they may not display the same ecological function as natural forest fragments. While cattle-grazing currently maintains these fragments, they were maintained historically by fire and are relatively long-term, stable habitats. Low overall cavity occupancy rates suggest that there is a surplus of cavities at Riske Creek. Northern Flickers and Red-naped Sapsuckers are abundant in the study area (Martin and Eadie 1999, Martin et al. 2002) and may saturate the habitat with holes. However, these holes are used infrequently and by few species. To estimate nest-site availability and selection for communities of cavity nesters, it is not sufficient to count the number of cavities in a stand, or to measure only the characteristics of occupied cavities. These results may overestimate cavity availability or provide inaccurate descriptions of nest-site preferences.

Chapter 3:
Nest site reuse patterns for a cavity nesting bird community in interior British Columbia

Introduction

Cavity nesting birds expend time and energy to excavate or compete for nest sites (Martin 1993, Newton 1994). These nest sites remain in the system for many years and are used multiple times. The rate of use of old cavities from year to year depends on costs and benefits of using old cavities and on cavity availability. The term “cavity reuse” here indicates that a previously excavated cavity was used for nesting and does not imply individuals used the same cavity repeatedly.

Primary excavators, such as Pileated Woodpeckers (*Dryocopus pileatus*) generally excavate a new cavity for nesting each year (Bull and Jackson 1995). New cavities may have fewer parasites and less debris (Moss and Camin 1970, Short 1979, Rendell and Verbeek 1996a, b), or may be less susceptible to predation (Sonerud, 1985, 1989, 1993; Nilsson et al. 1991). However, if excavators reused cavities, they would save considerable time and energy that could be allocated to reproduction. Nest-site reuse by primary excavators has been reported for Red-cockaded Woodpecker (*Picoides borealis*, Hooper et al. 1980, Harlow 1983, Conner and Rudolph 1995), Red-headed Woodpecker (*Melanerpes erythrocephalus*, Ingold 1991), Pileated Woodpecker (McClelland 1979, Bonar 2000) and Yellow-bellied Sapsucker (*Sphyrapicus varius,* Lawrence 1967, Kilham 1962). Nest cavity reuse is common for some Northern Flicker populations (*Colaptes auratus*; Ingold 1994, Holt 1996), but not for others (Lawrence 1967, Gutzwiller and Anderson 1986). In Rocky Mountain old growth forests of Montana, Red-naped Sapsuckers (*Sphyrapicus nuchalis*) reused 14% of old sapsucker cavities and 52% of sapsucker nest trees (McClelland and McClelland 2000).

Cavity reuse by weak excavators varies within and among species. Black-capped Chickadees (*Poecile atricapillus*) rarely reuse cavities, while Mountain Chickadees (*P. gambeli*) regularly do so (Hill and Lein 1988, Smith 1993, McCallum et al. 1999). All Mountain Chickadee nests and 52% of Red-breasted Nuthatch (*Sitta canadensis*) nests were in former Red-naped Sapsucker cavities in Montana (McClelland and McClelland 2000).

Secondary cavity nesters, by definition, must use existing cavities for reproduction. For these species, the presence of suitable nest sites limits population size (Scott 1979, Newton 1994, Holt and Martin 1997). The extent of nest site limitation depends on numbers of cavities available in relation to the demand. Cavity availability is influenced by several factors. These include rate of excavation and cavity reuse by excavators, rate of cavity loss from tree blow-down, and territoriality and competition among secondary cavity nesters. In addition, the willingness to reuse cavities might be influenced by levels of nest predation, parasitism and nest-site competition. Thus many of the same factors potentially determine rates of cavity reuse by all guilds.

It may be advantageous for cavity nesters using old holes to select cavities that were unoccupied the previous year. A lag of one or two years between occupants may enable cavity nesters to avoid experienced predators and the accumulation of nest parasites and debris. Predators learn the location of nest sites and revisit them (Sonerud 1985, 1989, 1993; Nilsson et al. 1991). The effects of old nest material on nest-site selection and reproductive success have not been proven conclusively. Some studies have shown that secondary cavity nesters are either indifferent to the presence of old nest material or may actually prefer nests containing old material (Davis et al. 1994; Mappes et al. 1994; Olsson and Allander 1995; Johnson 1996). Others suggest that some secondary cavity nesters prefer clean nest-sites (Rendell and Verbeek 1996a, b). For cavity nesters using old holes, there may be a trade-off between the advantages of selecting cavities with old nest material and increased predation risk in cavities occupied two years in a row.

Cavity reuse patterns are central to understanding the population ecology of cavity nesting birds in forest ecosystems. These patterns may be useful in formulating plans for cavity nester conservation and management. This study 1) details the rates of cavity reuse for guilds and species of a diverse cavity-nesting bird community in mixed forest stands in central interior British Columbia, 2) investigates relative rates of reuse among the three guilds of cavity nesters, and 3) examines characteristics of cavities, nest trees and forest stands that may influence reuse rates. I also determine whether there is a time lag in reuse of nest cavities.

Methods

Study area and design

Cavity use was monitored from 1995-1999 on 28 study sites in the Cariboo-Chilcotin region of interior British Columbia, Canada (51° 52'N, 122° 21'W; Figure 2.1). The region lies within the warm and dry Interior Douglas-Fir biogeoclimatic zone (Meidinger and Pojar 1991). It is characterized by mixed deciduous and coniferous forest embedded in a matrix of grassland and shallow ponds. In 1995, 11 sites were established, increased to 16 sites in 1996, and by 1997 and 1998 we were monitoring 28 sites. The study sites (7 to 35 ha in size) varied in character from continuous forest to two sites that were a series of aspen groves (forest islands; 0.2 to 5 ha) within the grassland matrix. All sites were mature forest (80-200 yr old), except four that were selectively logged for hybrid spruce (*Picea glauca* x *engelmannii*) and lodgepole pine (*Pinus contorta* var. *latifolia*) in early 1997. Predominant trees were lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), hybrid spruce and trembling aspen (*Populus tremuloides*). Additional details for study sites and project design are given in Martin and Eadie (1999) and Wiebe (2001).

Cavity nest location and habitat measurements

The cavity nesting community consisted of 32 bird and 12 mammal species (Martin and Eadie 1999). From 1 May to 31 July 1995-1999, we searched for active nests of all cavity nesters. Given the northern latitude of the study area, most migratory and resident cavity nesting species do not begin nesting until early May. Active cavities were located by looking or listening for excavation, by tapping or scraping at the base of cavity trees to detect occupants, by observing breeding behaviour, or by hearing begging nestlings. Cavities within reach of a ladder ($\leq$4 m) were visually inspected with flashlights and mirrors to establish nesting stage, status and fate. In addition to birds, cavities occupied by Red Squirrel (*Tamiasciurus hudsonicus*), Northern Flying Squirrel (*Glaucomys sabrinus*), Bushytail Woodrat (*Neotoma cinerea*) and Deer Mouse (*Peromyscus maniculatus*) were monitored. When active nests were found, cavities were assigned unique numbers and nest trees were tagged with numbered aluminum tags. After the cavity was vacated, data recorded included hole orientation, height above ground, entrance diameter, tree species, and diameter at breast height (DBH). Vertical depth was measured from the bottom of the cavity entrance to the cavity floor. Tree decay stage was classified on a scale from 1 through 8. Class 1 indicated a live healthy tree, class 2 a live unhealthy tree, and classes 3-8 were dead trees in advancing stages of decay (3 - a recently dead tree to 8 - a short soft stub in advanced decay; Thomas et al. 1979). Distance of the nest tree from the nearest grassland, lake or stream edge was also recorded.

From 1996 to 1999, previously occupied cavities were revisited a minimum of every 2 weeks, but usually twice weekly after 1996. Cavities that became unavailable due to tree blowdown were noted. Estimates of cavity reuse presented here are likely low because birds that initiated clutches and failed early in nesting may have gone undetected.

Habitat parameters were measured at three spatial scales: the nest tree, the nest plot (the nest tree at the centre) and site (multiple vegetation plots with plot centres at grid nodes). Several variables were recorded for all trees ≥12.5 cm DBH (British Columbia Ministry of Forests inventory standard) within an 11.2 m radius circle for both the nest plots and the vegetation plots on sites. These included: tree species, size (DBH), decay class, and the number of cavities (used or unused) present. Mean nest tree height on our study sites was 8.9 ± 0.08 m (n=502) and 51.5% of cavities (n=443) were ≤ 4m above ground (K. Martin, unpublished data). At sites with continuous forest, vegetation plots were spaced in a 100 x 100 m grid starting at a grassland or wetland edge and extending 500 m into the forest. In forest fragments, vegetation plots were spaced at least 100 m apart. Most sites covered an area that would include one or several territories of most cavity-nesting species present. Thus, habitat characteristics averaged over all vegetation plots on a site represents availability of nesting resources. For site-level characteristics, the density of trees (stems / ha), the number of cavities/ha, percent of aspen on site (based on the proportion of aspen stems/ha), and the proportion of vegetation plots within 50 m of forest edge were calculated. The latter variable reflects the amount of edge on sites and, therefore, patch size. In analyses of reuse in relation to habitat characteristics, each site was treated as a sample unit, rather than each individual cavity. Rates of reuse were calculated at the site level. Because all site vegetation plots were measured each year, we were able to monitor the annual removal of cavities on the sites.

Data selection criteria and analysis

Cavities >4m above the ground were not inspected to confirm activity. Thus, these were not included in analyses of cavity reuse. The set of active nest cavities available to be checked for reuse accumulated over the five-year study. Cavities that were destroyed between years were not included in further analyses. Any cavity from one year (Year A) that was checked in the subsequent year (Year B) was counted as a cavity reuse observation. In such cases, the initial year of use would be Year A and the subsequent year was Year B. However, if this cavity was checked again in the third year, the Year 2-3 set was also assigned a Year A and B, respectively. Nests located in 1995 and checked in all subsequent years would represent four cases of 2-year cavity rechecks. Nests found in 1996 had a maximum of three 2-year cases. Multiple sequences avoid the problem of year effects interacting with Year A-B sets, but are subject to concerns about non-independence. To avoid non-independence, a sub-sample of cavities and trees was selected for analyses of nest-site characteristics such that individual cavities and trees were included only once in those analyses. We developed systematic data selection criteria to ensure that the early years, with the smaller data set, were not randomly eliminated from the analysis. For cavities occurring in the dataset twice (two A-B sets), the first instance (i.e, the earliest A-B set) was selected for the first cavity, the second instance for the second cavity, the first case for the third cavity, and so on. For cavities in the dataset three times, the first instance was selected for the first cavity, the second for the second cavity, the third for the third cavity, the first for the fourth cavity, and so on. For cavities used twice within a season, the first occupant was included as the Year B class for the A-B set beginning the previous year. The second occupant was analysed as the Year A class for the following year. This was only a concern in analyses of guild and species reuse since cavities were included only once in analyses of nest-site characteristics, as described above.

Data were analysed using SPSS for Windows version 10.0.7 (SPSS Inc. 2000). Significance levels of $\alpha = 0.05$ were used. Continuous variables were tested for normality using one-sample Kolmogorov-Smirnov tests at the 95% confidence level (Zar 1984). Levene's test for homogeneity-of-variance was used to test the equality of variance among normally-distributed variables (SPSS Inc. 2000). Using independent sample t-tests, normally-distributed cavity and nest tree variables were compared between nest-sites that were occupied versus not occupied in Year B. Non-normally distributed variables were compared using Mann-Whitney *U* tests. Chi-square tests were used to examine categorical cavity and nest tree variables in relation to cavity reuse. Backward step-wise logistic regression was used to identify cavity and tree variables associated with reuse. Cavity variables in the logistic regression were height above ground, vertical and horizontal depth, hole entrance area, and orientation (N, W, S or E). Nest tree variables in the analysis were distance to edge, DBH, health category (live or dead), species (aspen or conifer) and number of cavities in the tree (1 or >1). To determine which habitat variables were associated with cavity reuse, we performed a forward stepwise multiple linear regression comparing rate of cavity reuse with several site level independent variables. Rate of reuse was calculated as proportion of cavities on each site that were reused. Variables in the regression were percent edge on sites, density of stems ≥12.5 cm dbh / ha, cavity density and percent aspen. Variables required a significance of 0.05 to enter, and to remain in, the models.

Results

A total of 193 individual cavities was checked for reuse in at least two sequential years from 1995 to 1999. Thirty-seven cavities were followed for all 5 years (i.e., four potential reuse cases / cavity), 25 cavities for 4 years, 48 cavities for 3 years, and 83 cavities were checked in two sequential years. These gave a total of 402 individual observations of Year A to Year B reuse. Fifteen of the 193 cavities (8%) were destroyed during the course of the study. Cavities were more likely to be occupied two years in a row rather than remaining empty for one or more years; of 246 cases where cavities were occupied in Year A (178 individual cavities), 37% were used again the next year (Year B), while only 21% of 141 cavities that were unoccupied in Year A were reused in Year B ($\chi^2_1 = 10.79$, $P = 0.001$). Thus, there was no support for the lag hypothesis in cavity reuse.

i) Reuse according to guild and species

When guild of the Year A occupant was examined in relation to use in Year B, the three guilds differed as to whether their cavities were reused ($\chi^2_2 = 15.02$, $P = 0.001$, n = 246, Figure 3.1). Cavities previously used by secondary cavity nesters (SCN) had the highest reuse rate (48%). This was higher than for cavities previously used by weak excavators (WCE; 17%; $\chi^2_1 = 10.6$, $P = 0.001$) or by primary excavators (PCE; 28%; $\chi^2_1 = 7.6$, $P = 0.006$; Figure 3.1). Guild of occupant in Year B differed according to the guild of the occupant in the previous year (Year A, $\chi^2_4 = 23.85$, $P < 0.001$, Figure 3.1). Cavities first recorded as used by SCNs and WCEs were reused more often by the same species in Year B, than were cavities of PCEs (Figure 3.1). Seventy percent of 20 cavities occupied by woodpeckers in Year A were reused by other guilds in Year B, whereas extra-guild reuse accounted for only 15% of SCN and 17% of WCE nest cavities (Table 3.1).

Patterns of cavity reuse varied considerably among species (Table 3.1). Among the primary excavators, Northern Flicker nests were reused most frequently (36% reuse rate). Flickers were the only woodpecker that reused their own nests to any extent (11%). In terms of extra-guild reuse, about 25% of flicker nests were reused by other guilds, followed by 12.5% of Red-naped Sapsucker nests. There was little reuse of other woodpecker cavities, but this pattern may change with a larger sample of nests between years, particularly for Pileated Woodpeckers. Cavity reuse among the three species of weak excavators varied considerably. While just 9% of Mountain Chickadee cavities were reused, 36% of Red-breasted Nuthatch cavities were reused, either by nuthatches or by Mountain Chickadees. Among secondary cavity nesters with sufficient sample sizes ($n \geq 10$), European Starling (*Sturnus vulgaris*) nests were the most frequently reused (66%), primarily by starlings. Red Squirrel nests were reused the least frequently (10%, Table 3.1, Fig. 3.2).

ii) Nest cavity and tree characteristics

Characteristics of 185 individual cavities (representing 185 A-B cases), in 163 individual trees, were analysed. Of these, 94% were in trembling aspen, 4.3% were in lodgepole pine, 1.2% were in Douglas-fir, and 0.5% were in spruce. When conifer species were pooled and compared with aspen, only the latter was associated with cavity reuse ($\chi^2_1 = 5.28$, $P = 0.02$). Using independent sample t-tests, cavity entrance area and vertical cavity depth differed significantly between reused and not reused cavities (Table 3.2). Reused cavities were deeper and had larger entrances. There was no association between cavity reuse and tree health, number of cavities in the nest tree, or cavity orientation. Similar results were achieved using a multivariate approach. Using logistic regression to determine which suite of cavity and nest tree characteristics best predicted reuse, entrance area (-2 Log Likelihood = 6.28, $P = 0.012$), distance to edge (-2 Log L = 4.43, $P = 0.035$), and tree species (-2 Log L = 9.29, $P = 0.002$) were significant predictors in the model.

iii) Habitat and site-level characteristics

Cavity reuse rates were calculated for sites with at least five cavities checked in two consecutive years (5 -157 cavities per site; 10 sites). Only percent edge, which ranged from 12.5 to 100% across sites, entered the model ($r^2 = 0.43$, $F = 5.99$, $P = 0.04$). Sites with a higher proportion of edge habitat had higher rates of cavity reuse.

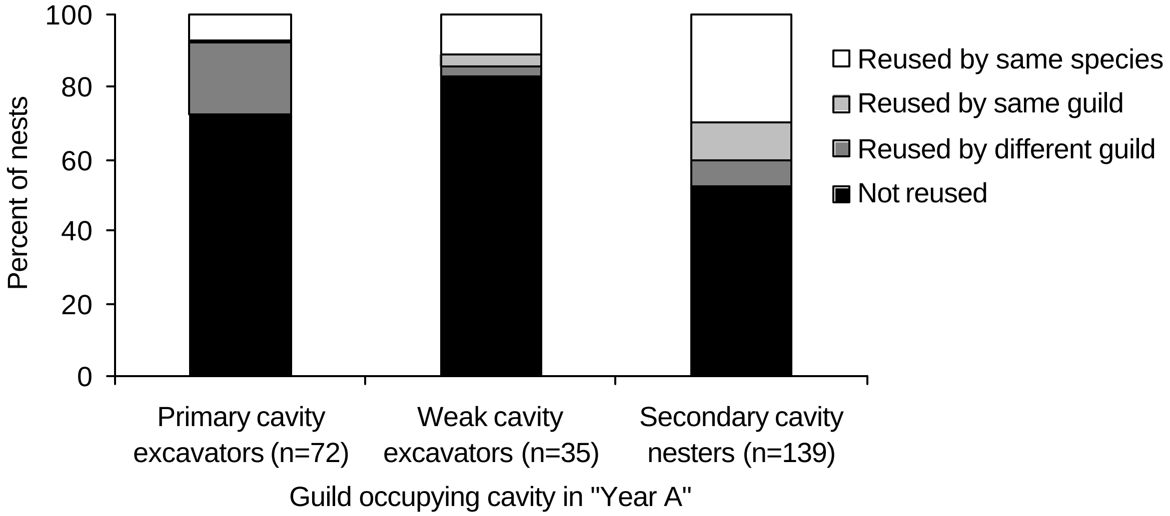

Figure 3.1. Proportion of active nest cavities reused in a subsequent year in relation to cavity nesting guild in mixed forest stands in interior British Columbia, Canada.

Table 3.1. Summary of reuse of nesting cavities by cavity-nesting vertebrates in mixed forests in interior British Columbia.

				Cavities used in following year		
Occupant in Year A	**Total (n)**	**Cavities surviving to following year (%)**	**Cavities not used in following year (%)**	**By same species (%)**	**By same guild (%)**	**By different guild (%)**
A. Primary cavity excavators						
Northern Flicker (*Colaptes auratus)*	48	91.7	63.6	11.4	0.0	25.0
Red-naped Sapsucker (*Sphyrapicus nuchalis)*	24	100.0	87.5	0.0	0.0	12.5
Downy Woodpecker (*Picoides pubescens)*	1	100.0	100.0	0.0	0.0	0.0
Hairy Woodpecker (*Picoides villosus)*	1	100.0	100.0	0.0	0.0	0.0
Three-toed Woodpecker (*Picoides tridactylus)*	2	100.0	50.0	0.0	50.0	0.0
Total primary cavity excavators	76	94.7	72.2	6.9	1.4	19.4
B. Weak cavity excavators						
Black-capped Chickadee (*Poecile atricapillus)*	2	100.0	100.0	0.0	0.0	0.0
Mountain Chickadee (*Poecile gambeli)*	23	95.7	90.9	4.5	0.0	4.5
Red-breasted Nuthatch (*Sitta canadensis)*	12	91.7	63.6	27.3	9.1	0.0
Total weak excavators	37	94.6	82.9	11.4	2.9	2.9
C. Secondary cavity nesters						
Bufflehead (*Bucephala albeola)*	2	100.0	50.0	0.0	0.0	50.0
American Kestrel (*Falco sparverius)*	12	91.7	54.5	27.3	18.2	0.0
Tree Swallow (*Tachycineta bicolor)*	26	96.2	76.0	12.0	4.0	8.0
Mountain Bluebird (*Sialia currucoides)*	38	97.4	51.4	27.0	16.2	5.4
European Starling (*Sturnus vulgaris)*	54	98.1	34.0	49.1	7.5	9.4
Bushytail Woodrat (*Neotoma cinerea)*	1	100.0	100.0	0.0	0.0	0.0
Red Squirrel (*Tamiasciurus hudsonicus)*	10	100.0	90.0	0.0	10.0	0.0
Total secondary cavity nesters	143	97.2	52.5	30.2	10.1	7.2
Grand Total	256	96.1	62.6	20.7	6.5	10.2

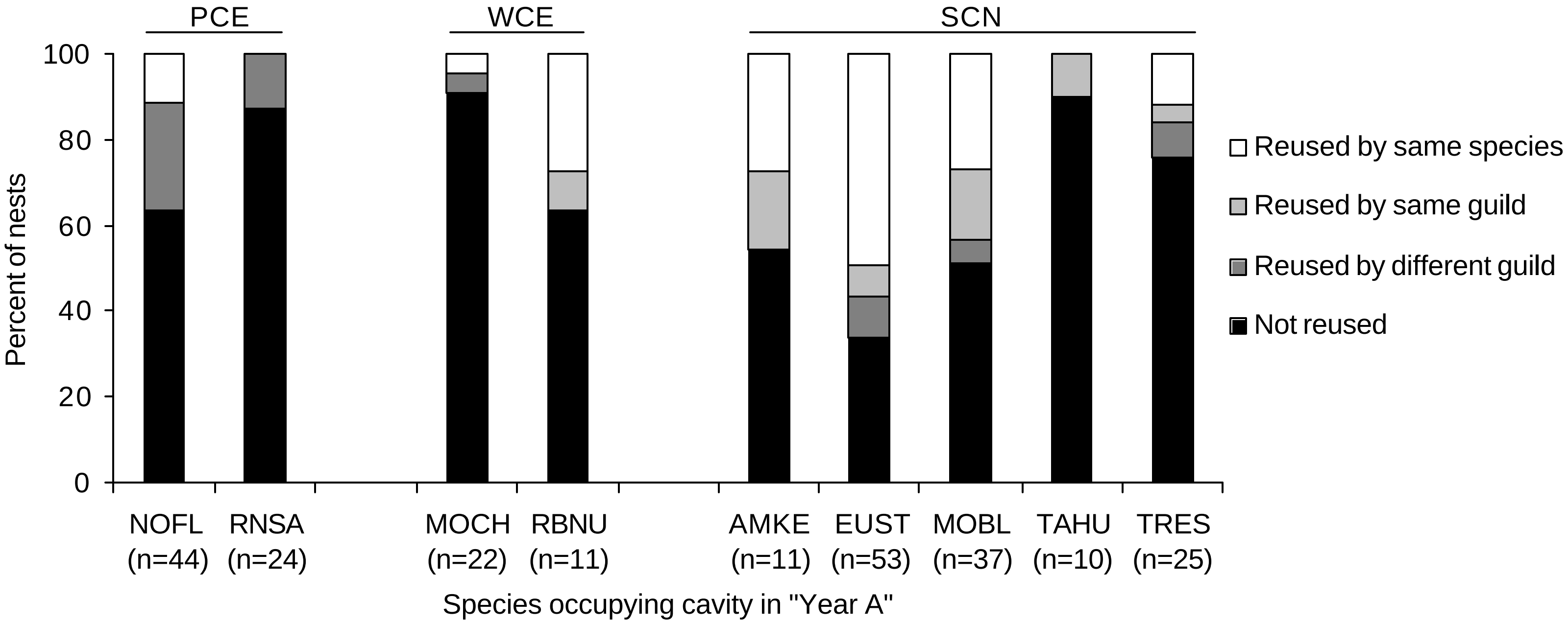

Figure 3.2. Reuse of cavities in a subsequent year that were occupied by core species of primary cavity excavators (PCE), weak cavity excavators (WCE) and secondary cavity nesting (SCN) guilds in interior British Columbia. Species name codes: NOFL - Northern Flicker, RNSA - Red-naped Sapsucker, MOCH - Mountain Chickadee, RBNU - Red-breasted Nuthatch, AMKE - American Kestrel, EUST - European Starling, MOBL - Mountain Bluebird, TAHU - Red Squirrel, TRES - Tree Swallow.

Table 3.2. Means of cavities that were reused and not reused by cavity nesting birds and mammals in interior British Columbia, with results of univariate *t*-tests and Mann-Whitney *U* tests. See text for results of logistic regression analysis.

	Reused		**Not reused**		
	Mean ± SE	n	Mean ± SE	n	*Test statistic*[a] (*P*)
Cavity characteristics					
Cavity height above ground (m)	2.5 ± 0.11	54	2.5 ± 0.10	109	2801.0 (0.62)
Entrance hole area (cm^2)	33.8 ± 5.62	38	22.6 ± 1.34	93	1216.5 **(0.005)**
Vertical depth (cm)	26.2 ± 2.53	34	19.0 ± 1.67	91	980.5 **(0.002)**
Horizontal depth (cm)	13.8 ± 0.87	36	12.2 ± 0.50	93	1.68 (0.10)
DBH (cm)	31.6 ± 1.26	54	29.4 ± 0.91	108	1.41 (0.16)
Tree characteristics					
Distance to forest edge (m)	8.5 ± 1.62	50	19.5 ± 3.50	101	2129.5 (0.11)

[a] *t*: Horizontal depth, DBH
U: Cavity height, entrance area, vertical depth, distance to edge

Discussion

Cavity reuse within and across guilds

Few studies have examined patterns of cavity reuse for multi-guild communities of cavity-nesting birds, particularly those using natural nest sites. Overall, cavity reuse by excavators was low compared to secondary cavity nesters (SCNs). Northern Flickers were the only woodpecker that reused cavities with any regularity. Cavity reuse rates of 11% by Northern Flickers at Riske Creek were low compared to 29% reuse found by Sedgwick (1997) and 50% found elsewhere for flickers (Ingold 1994). In Colorado cottonwood bottomlands, 59% of woodpecker cavities were reused compared to 53% reuse for secondary cavity nesters, but SCN cavities werereused by the same species more often than woodpecker nests (Sedgwick 1997).

Competition and availability of suitable nest trees may explain why reuse rates were highest for the most abundant woodpeckers. Although similar numbers of detections were recorded for Northern Flickers and Red-naped Sapsuckers in point count censuses on the study sites (K. Martin, unpublished data), cavity reuse rates differed for these species. Sapsuckers chose live trees (decay class 1 and 2), which represented about 90% of trees present. Sapsuckers used trees an average of 29 m from forest edge. In contrast, over 60% of flicker nests were in dead trees with decay class 3 to 6 (10% of trees present) and were an average of 12 m from edge (K. Martin unpublished data). Thus, availability of suitable dead trees close to edges for excavation may be sufficiently low for flickers in this area to encourage nest cavity reuse. In a managed landscape, with few large decayed trees, Holt (1996) found cavity reuse rates of 44% for flickers.

Northern Flickers are subject to strong competition from European Starlings in most parts of their range (Gutzwiller and Anderson 1987, Moore 1995, Ingold 1998), including interior British Columbia (Erskine and McLaren 1976, Peterson and Gauthier 1985). Flickers might reuse existing cavities after starlings usurp their newly excavated hole, especially if it is too late in the season to excavate another one. The late arrival of migratory breeding woodpeckers might increase tendencies of primary excavators to reuse old cavities. Flickers and sapsuckers are the main migratory woodpeckers in this region, and interestingly, had the highest reuse rates.

At the community level, Northern Flickers provided the most cavities for other species (Martin and Eadie 1999). There is limited reuse data for Pileated Woodpecker cavities on these sites. However, a concurrent study found extensive use of Pileated Woodpecker cavities by cavity-nesting ducks, particularly Barrow's Goldeneye (*Bucephala islandica*; M. R. Evans, unpublished data). In Alberta, Pileated Woodpecker cavities were reused by 18 other species (Bonar 2000). Thus, our data likely underestimate the importance of Pileated Woodpecker cavities in this system. Given their abundance, however, Northern Flickers represent the core species in the nest web of the cavity nesting vertebrate community in Interior Douglas-fir forest ecosystems (Martin and Eadie 1999).

Reuse of weak excavator (WCE) nests was lower than woodpecker cavities and primarily within guild, usually the same species. Weak excavators may be less able to compete with larger secondary cavity-nesters for woodpecker cavities and thus reuse their own holes. WCE cavities were shallower with smaller entrances than most cavities used by secondary cavity nesters. This may account for the low rate of extra-guild reuse (K. Martin, unpublished data). The considerable variation in cavity reuse among the three species of WCEs may reflect differences in excavation abilities. Mountain Chickadees tend to use existing cavities (McCallum et al. 1999). In our study, Mountain Chickadees used natural cavities or they reused sapsucker cavities, while nuthatches and Black-capped Chickadees excavated their own holes. We observed no reuse of Black-capped Chickadee cavities by Mountain Chickadees, or vice versa. This supports the ecological segregation hypothesis suggested by Hill and Lein (1988) to avoid competition for nesting and foraging sites when these species occur sympatrically.

Secondary cavity nesters - the 'cavity consumers'

As expected, secondary cavity nesters had the highest rates of cavity reuse among the three guilds. However, there was much variation in reuse rates across species. Reuse rates were high for European Starling cavities, moderate for those of Mountain Bluebirds and Tree Swallows (*Tachycineta bicolor*), and low for Red Squirrels. Rates of reuse varied from 44 to 67% in a community of secondary cavity nesters in Poland (Wesolowski 1989). On our study area, excavator species were varied and abundant, and 92% of cavities present in one year were available the next. Thus, suitable cavities may not be limiting, reducing the need for cavity reuse among secondary cavity nesters. However, we recognize our reuse rates are minimum estimates as we undersample cavity nesting raptors (owls, American Kestrel) and mammals (squirrels, woodrats and bats). Some of these cryptic secondary cavity-nesting species are abundant and may influence cavity availability in the community. In addition to nesting and roosting, mammals sometimes fill cavities with nesting material or cones rendering them unusable for other cavity nesters (pers. obs.). The role of cavity nesting mammals as consumers of cavities and competitors with cavity nesting birds requires further study.

Nest cavity, nest tree and habitat characteristics

We observed highest reuse of large and deep cavities. Cavity entrance size and volume are important factors because they influence the types of species that can use cavities. Cavity size might also influence reproductive success, competition and predation. Elsewhere in the region, cavity volume and hole entrance size were the most important variables determining cavity occupancy for Northern Flickers, European Starlings, Tree Swallows and Bufflehead (Peterson and Gauthier 1985). A larger cavity area may allow larger clutch sizes (Karlsson and Nilsson 1977, Rendell and Robertson 1989, Robertson and Rendell 1990, Rendell and Verbeek 1996a, Stewart and Robertson 1999). Large cavities may also allow better heat-dissipation on hot days (Alatalo et al. 1988) and reduce competition for space and feeding positions among siblings (Slagsvold 1989). However, larger cavities may also experience higher predation (Zeleny 1977, Moed and Dawson 1979, Robertson and Rendell 1990). For a larger sample of flickers in our area, reproductive success in two years was not related to cavity volume or microclimate, and larger cavities had lower predation rates (Wiebe 2001). Given these data, it appears that the benefits associated with larger cavities outweigh the costs, at least for flickers.

Aspen trees were strongly selected for nesting on our study sites (Martin and Eadie 1999), and cavities in aspen had higher reuse rates than those in conifers. Aspen may be preferred for excavation by woodpeckers and weak excavators because it is susceptible to heartwood rot. This decay provides a soft substrate for excavation while retaining a firm shell of sapwood, giving stability and protection for the cavity (Kilham 1971, Conner et al. 1976, Harestad and Keisker 1989).

Surprisingly, we did not find that nest tree diameter, cavity orientation, or stage of decay were significant predictors of cavity reuse. The stage of nest tree decay may affect both cavity microclimate and the ability of predators to access nests. Flicker cavities in more decayed trees had higher maximum temperatures and greater daily temperature fluctuations, but thermal conditions and reproductive success were uncorrelated (Wiebe 2001). Black-capped and

Carolina Chickadees (*Poecile carolinensis*) had higher nest success in trees with harder wood and thicker walls, which may prevent predators from chewing or ripping open cavities (Albano 1992, Christman and Dhondt 1997).

Site-level characteristics and cavity reuse

One might expect higher predation risk and greater microclimatic fluctuations in small forest patches and near edge than in the forest interior. However, cavity nesters did not avoid edges, as we observed higher reuse rates on sites with more edge. Nests located close to woodland edges should benefit aerial or open habitat insectivores, such as Tree Swallows, Mountain Bluebirds and Northern Flickers. In our study, these species tended to nest within 15 m of forest edge (K. Martin unpublished data). European Starlings, in particular, strongly prefer nests in edge habitats (Peterson and Gauthier 1985, Kerpez and Smith 1990, Dobkin et al. 1995). Flickers were the dominant excavator with the highest reuse among PCEs and were associated with grassland habitat. Thus, higher cavity reuse on forest edges may be due to nest site preferences of Northern Flickers and European Starlings.

Interspecific competition in cavity-nesters may vary with distance to forest edge. Tree Swallows avoided competition with House Wrens (*Troglodytes aedon*) and Eastern Bluebirds (*Sialia sialis*) by nesting farther from the edge in eastern Ontario (Rendell and Robertson 1990). Starlings dominated riparian areas with edge, and were strong competitors with Northern Flickers, Mountain Bluebirds, Tree Swallows and other cavity-nesting species (Gutzwiller and Anderson 1987). In the Oregon Great Basin, Tree Swallows nested primarily in sapsucker cavities near woodland edges, possibly to avoid competition with starlings for flicker cavities (Dobkin et al. 1995). In the latter study, swallows occupied flicker cavities located more than 15m from the edge, cavities that presumably were unattractive to starlings. In our study, there may be sufficient cavities on edges for most species to nest near forest edge (K. Martin, unpublished data). Cavity reuse facilitates the option of nesting near forest edge.

We found no support for the cavity reuse lag hypothesis, at least in the short term. Cavities used in one year were twice as likely to be reused in a subsequent year compared to those that remained vacant for a year. The preference for cavities that were occupied the previous year may be due to nest-site fidelity after successful breeding as reported for Bufflehead (*Bucephala albeola*, Gauthier 1993) and Red-cockaded Woodpecker (Jackson 1994). Sequential reuse of cavities might also reflect desired cavity or habitat characteristics in good proximity to other required resources. Cavity reuse may be influenced by factors other than cavity availability and suitability. For example, secondary cavity nesters may avoid using vacant cavities if woodpeckers excavate new cavities nearby. The role of woodpeckers as predators on nests of other cavity-nesters needs to be determined for our system. Walankiewicz (1991) reported Great Spotted Woodpeckers (*Dendrocopus major*) and other unidentified woodpeckers destroying nests of Collared Flycatchers (*Ficedula albicollis*) in Poland. Christman and Dhondt (1997) reported destruction of Black-capped Chickadee nests by either Pileated Woodpecker or Red-bellied Woodpecker (*Melanerpes carolinus*). Flickers were implicated in the destruction of Tree Swallow nests (Rendell and Robertson 1989), and in Sweden, woodpeckers were suspected to be the main predators of tits (*Parus* sp.) nesting in boxes (Nilsson 1984). Thus, a simple count of vacant holes will overestimate cavity availability.

A range of nest-site attributes, from fine-scale cavity and nest tree characteristics to larger-scale habitat variables, determined cavity reuse patterns on our study sites. This indicates that nest-site selection in cavity nesters is not based solely on cavity characteristics. The nest site context such as proximity to foraging habitat is likely important. Similar patterns were observed for open cup-nesting forest songbirds in interior British Columbia. In that case, nest sites were selected primarily on habitat or stand features, rather than characteristics of the nest tree or shrub (Easton and Martin 2001).

Summary

Cavity nesters on our study sites reused holes less often than reported elsewhere (usually in harvested forest landscapes). In general, however, our guild level patterns were consistent with other studies. Low reuse rates may be possible given the richness of excavator populations in the British Columbia interior, and the abundance of Northern Flickers, the core excavator species. However, actual reuse rates may be higher than we report here because we underestimated cavity use by cryptic cavity consumers, such as cavity nesting mammals and raptors.

Harvested forests often have a reduced supply of suitable nesting cavities. Nest-site reuse may mitigate some effects of forest removal on cavity nesting species in interior forest ecosystems. However, we need a better understanding of how cavity reuse impacts reproductive success, and the role of cavity competitors in the system. Comprehensive data on rates of cavity creation and removal across a range of forest stand types is also necessary.

Chapter 4:
General Conclusions

Thesis summary

Nest cavities created by woodpeckers are an essential commodity for secondary cavity nesting species. The production and use of holes results in a community hierarchy, or nest web, similar in structure to a food web (Martin and Eadie 1999). Most woodpeckers excavate at least one new cavity per year (Thomas et al. 1979, Stenberg 1996, McClelland and McClelland 2000). If the rate of cavity creation by excavation and natural processes exceeds the rate of loss (due to windthrow, destruction by predators, and other factors), a surplus of cavities accumulates in the landscape. These cavities remain in the system for several years and can be used multiple times. To understand nest-site requirements of cavity-nesters, it is necessary to determine cavity use in relation to cavity availability in the habitat, and to examine the dynamics of cavity re-occupation in the community. This was the focus of my thesis research, which I presented in Chapters 2 and 3.

Characteristics of occupied nest-sites

Cavity use and reuse rates may have been higher in fragments than in continuous forest for several reasons. Small forest patches may offer reduced nest predation rates (Tewksbury et al. 1998, Storch 1991). Second, the most abundant secondary cavity nesters in the area (Mountain Bluebirds, Tree Swallows, European Starlings), as well as the most common excavator (Northern Flicker), were associated with open habitats. Finally, I may have under-sampled some forest-associated species that were either cryptic (small mammals, owls) or had large territories (Pileated Woodpeckers, Three-toed Woodpeckers, Black-backed Woodpeckers, Hairy Woodpeckers). Bonar (2000) found average cavity-tree density on Pileated Woodpecker (*Dryocopus pileatus*) territories in Alberta was 1.3 per square kilometre. Thus, the area I surveyed may not have been large enough to encompass cavities for area-sensitive species.

Cavities created by Northern Flickers were used more often than those created by Red-naped Sapsuckers. Flicker cavities are larger than sapsucker holes and can accommodate a broader range of species. They may also allow larger clutch sizes (Karlsson and Nilsson 1977, Stewart and Robertson 1999) and increase thermoregulation efficiency and feeding ability of nestlings (Van Balen 1984, Alatalo et al. 1988, Slagsvold 1989). For these reasons, competition for cavities created by flickers may be more intense than for those excavated by sapsuckers. However, flicker cavities were abundant at Riske Creek, suggesting that flickers saturate the habitat with holes. Competition for nest-sites is influenced by nest-site availability, and where cavities are abundant competition should be low (Lindell 1996). The influence of cavity turnover (creation and loss) rates on cavity availability and nest-site competition needs to be examined.

Nest-site selection by cavity-nesters varied between 2000 and 2001. This may be due to small sample sizes in my analyses, or to annual variation in the composition of the cavity nesting community. A larger study of cavity nesters at Riske Creek, conducted between 1995-2001, showed that species diversity and abundance fluctuated between years at individual sites, but was stable at the landscape level (Martin and Eadie 1999; and for all years, K. Martin, unpubl. data). This local instability may result in apparent variation in nest-site selection patterns, and highlights the need for multi-year, large-scale studies of cavity-nesting community dynamics.

While cavities were abundant in forest fragments, those habitats were not saturated with nests. Although it is possible that unoccupied cavities were unsuitable, I found few differences between occupied and unoccupied holes. Birds occupying cavities may have excluded individuals from remaining cavities. Additionally, food availability, rather than cavity abundance, may limit the number of birds that the habitat can support. Finally, returning birds may avoid nest-sites they used the previous year if they were unsuccessful. While I did not have data to address these hypotheses, they could be tested using experiments such as nest box addition, cavity removal (blocking), and food supplementation.

Small mammals and owls were under-sampled in my study and their role in cavity nesting community dynamics requires further examination. Nests of Red Squirrels, Northern Flying Squirrels (*Glaucomys sabrinus*), Northern Saw-whet Owls (*Aegolius acadicus*), Barred Owls (*Strix varia*) and others are difficult to locate because of the cryptic behaviour and early breeding in these species. Breeding by small mammals and owls begins as early as March and may be completed by May. Winter use of cavities by these species as roosts and food storage sites should also be examined because these cavities may not be vacated in time for early spring nest-site selection by other species. Some small mammals such as Red Squirrels and Deer Mice (*Peromyscus maniculatus*), and raptors such as American Kestrels, prey on cavity-nesting adults, eggs or nestlings, in addition to competing with these species for cavities (Robertson et al. 1992, Power and Lombardo 1996). This interesting dynamic is largely unexplored in these communities.

Predation risk can influence nest-site selection and a better understanding of the predator assemblage is needed for this community. 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 at Riske Creek (Evans et al. 2002, K. Wiebe, unpubl. data). Identification of hairs left at the entrances of some depredated nests suggests that Red Squirrels and Marten (*Martes americana*) prey on eggs, nestlings and possibly adults in cavities (Evans et al. 2002, K. Aitken and K. Martin, unpubl. data). Other potential nest predators recorded in the area include weasels (*Mustela* spp.), chipmunks (*Eutamius* spp.), American Crows (*Corvus brachyrhynchos*), and carpenter ants (*Camponotus* spp; Daily 1993, Power and Lombardo 1996). Several species of woodpeckers, including Northern Flickers and Pileated Woodpeckers, prey on eggs and nestlings of cavity-nesters (Robertson et al. 1992, Christman and Dhondt 1997). Understanding predation pressures on cavity-nesting communities will help explain nest-site selection patterns.

Patterns of nest-site reuse

Cavity reuse rates varied among guilds and species in the cavity-nesting community at Riske Creek. Cavities previously used by secondary cavity nesters had the highest rates of reuse, while those of weak excavators were reused the least. Surprisingly, only 28% of cavities used by woodpeckers were occupied the following year. Woodpeckers use old cavities for roosting during the breeding season, possibly excluding other birds from nesting in them (Moore 1995, Bonar 2000). Because woodpeckers prey on other cavity nesters (Nilsson 1984, Walankiewicz 1991, Christman and Dhondt 1997), weak excavators and secondary cavity nesters may avoid using recently occupied woodpecker holes.

Cavities were used two years in a row, rather than remaining empty for a year between occupants. This suggests that commonly cited disadvantages of cavity reuse (increased predation risk and parasite loads) are less important in the Cariboo-Chilcotin than in other systems. The abundance of Red Squirrels and other nest predators may be lower in forest fragments (Tewksbury et al. 1998), reducing the likelihood of predators visiting cavities from year to year. The effects of old nest material on nest-site selection may depend on the types of ectoparasites present and their ability to overwinter in old nests. Adult blowflies (*Protocalliphora* spp.), whose larvae parasitize nestlings of Tree Swallows, bluebirds, and other cavity nesters (Pinkowski 1977, Rendell and Verbeek 1996c), do not overwinter in nests (Darling and Thomson-Delaney 1993). Johnson (1996) found that House Wren (*Troglodytes aedon*) chicks raised in boxes containing old material did not have higher ectoparasite loads than those in cleaned boxes. Eastern Bluebirds (*Sialia sialis*), Pied Flycatchers (*Ficedula hypoleuca*) and tits (*Parus* spp.) prefer or are indifferent to old nest material (Davis et al. 1994, Olsson and Allander 1995). Additionally, some cavity nesters use nest material such as vegetation or feathers that may deter parasites (Clark 1991, Winkler 1993). I have observed starlings at Riske Creek placing green leaves in cavities between first and second nest attempts.

Future studies should examine nest cavity reuse at the individual level, by banding adults and nestlings. This would provide a better understanding of the variation in patterns of nest site fidelity and cavity selection, and how past breeding attempts influence nest-site fidelity. Other studies have found that birds are more likely to reuse a nest site if they were successful the previous year (Gauthier 1993, Power and Lombardo 1996, Eadie et al. 2000); however, most of these studies examined nest boxes rather than natural cavities. Nest-site fidelity among Northern Flickers is being studied in natural cavities at Riske Creek (K.L. Wiebe, unpubl. data), but no studies have examined nest-site fidelity among multiple species in a community. This may be because capturing adult cavity-nesters is time-consuming and each species requires a different technique. Banding nestlings in cavities is also difficult and usually requires that a door be cut in the nest tree. However, this information is critical to understanding the dynamics of nest cavity reuse in this community. It would help to explain why some species, particularly secondary cavity nesters, vary in their rates of nest-site reuse.

Conservation and management implications

Wildlife management guidelines for British Columbia forests emphasize some attributes that are important to cavity nesters. These guidelines stress the importance of hardwood trees for wildlife and recommend retention of live trees for wildlife tree recruitment (BC Ministry of Forests 1995). Other jurisdictions nationally and internationally have similar guidelines, including Ontario and Norway (James 1984, Aanderaa et al. 1996). The Food and Agriculture Organization of the United Nations (FAO) has recognised the importance of retaining dying trees as cavity nester habitat (FAO 2000). At Riske Creek, cavity nesters preferred holes in live unhealthy aspen (Martin and Eadie 1999). However, in practice, aspen trees are often cleared during logging operations, either for firewood or for sale to pulp mills. Aspen that remains, either within cutblocks or along riparian buffer strips, may fall down within the first year or two after harvesting if they are not provided with conifer windbreaks. To manage for cavity nesting birds, live and dead aspen should be retained in patches throughout the harvest area and harvest prescriptions should attempt to minimize the risk of subsequent blowdown. A variety of age-classes of aspen should be retained over the landscape for future recruitment as cavity trees.

Concern about the effects of habitat fragmentation and edge on reproductive success of forest birds has increased in recent years. Birds nesting near forest edges often suffer increased nest predation and reduced breeding success (Sandstrom 1991, Andrén 1992, Kuitunen and Makinen 1993, Zegers et al. 2000). However, little work has focussed on reproductive success in natural or long-term edges, such as those found at Riske Creek. Current research provides conflicting results. For example, De Santo and Willson (2001) found higher predation of artificial nests at forest-wetland edge than in forest interior or in wetland habitats, while Poyså et al. (1997, 1999) found no relationship between predation of Common Goldeneye (*Bucephala clangula*) nests and distance to forest-lake edge. There was no relationship between distance to grassland or lake edge and predation of Barrow's Goldeneye and Bufflehead nests at Riske Creek (M.R. Evans, unpubl. data). Future work should compare nest failure rates among natural forest fragments, interior forests and forest-grassland edges to determine whether fragments act as sources or sinks for cavity-nester populations.

My results indicate that large-scale habitat characteristics such as proximity to foraging habitat are better predictors of nest-site use than cavity or microhabitat characteristics. Thus cavity-nesting communities need to be managed at a larger scale than individual nest trees or cavities. Managing at the microhabitat or cavity scale may harm species with large territory sizes and home ranges, including many woodpecker species. Because cavity abundance does not reflect cavity use, a simple count of cavities may not indicate the ability of a habitat to sustain cavity-nester populations. Finally, while forest fragments at Riske Creek had high nest densities compared to continuous forest, they were characterized by long-term, natural edges adjacent to native grassland. While multi-tree reserves in harvested landscapes can mitigate some of the effects of forest cutting (Schieck and Hobson 2000), they may not display the same ecological function as natural forest fragments.

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APPENDIX I

Mean nest-site characteristics of cavity-nesting species in forest fragments near Riske Creek, BC, in 2000 and 2001.

a) 2000:

Characteristic[a]	Northern Flicker Mean ± SE[b] (n)	Mountain Bluebird Mean ± SE (n)	Tree Swallow Mean ± SE (n)	European Starling Mean ± SE (n)	Mountain Chickadee Mean ± SE (n)	Red Squirrel Mean ± SE (n)	Unused Mean ± SE (n)
Cavity height (m)	1.7 ± 0.26 (15)	2.0 ± 0.44 (9)	2.7 ± 0.30 (13)	2.6 ± 0.22 (25)	2.9 ± 0.34 (6)	2.4 ± 0.56 (6)	2.8 ± 0.12 (110)
Vert. depth (cm) **	43.5 ± 8.05 **a** (14)	11.0 ± 1.31 **c** (9)	13.5 ± 2.69 **bc** (11)	21.0 ± 1.73 **b** (23)	12.5 ± 1.12 **c** (6)	22.5 ± 23.4 **abc** (5)	18.0 ± 2.97 **bc** (82)
Horiz. depth (cm) **	15.2 ± 1.44 **a** (15)	10.6 ± 1.21 **abc** (9)	11.0 ± 0.82 **bc** (12)	13.7 ± 1.09 **ab** (24)	9.5 ± 0.74 **c** (6)	16.2 ± 3.67 **abc** (5)	12.5 ± 0.51 **abc** (87)
Ent. area (cm^2) *	32.0 ± 1.33 **a** (13)	25.9 ± 3.94 **ab** (9)	23.6 ± 4.71 **ab** (12)	25.9 ± 1.56 **ab** (24)	12.4 ± 3.32 **b** (6)	19.8 ± 14.9 **ab** (6)	23.7 ± 2.21 **ab** (86)
DBH (cm) *	36.7 ± 2.55 (15)	30.1 ± 2.43 (9)	28.0 ± 2.73 (13)	34.2 ± 1.77 (25)	24.0 ± 2.66 (6)	29.2 ± 5.91 (6)	30.9 ± 0.99 (109)
DCH (cm) **	33.2 ± 2.18 **a** (14)	25.0 ± 3.04 **ab** (9)	27.3 ± 2.78 **ab** (12)	36.2 ± 2.00 **a** (24)	21.9 ± 1.93 **b** (6)	29.5 ± 5.13 **ab** (6)	29.0 ± 1.31 **ab** (84)
Tree ht (m)	8.0 ± 1.33 (15)	9.0 ± 1.27 (9)	9.7 ± 0.79 (13)	11.0 ± 1.00 (25)	10.2 ± 0.62 (6)	14.0 ± 2.53 (6)	9.0 ± 0.43 (109)
Crown ratio *	0.4 ± 0.06 (7)	0.7 ± 0.07 (4)	0.5 ± 0.03 (9)	0.5 ± 0.05 17	0.6 ± 0.07 (4)	0.5 ± 0.10 (3)	0.6 ± 0.02 (44)
Obstruction dist (m) *	1.6 ± 1.00 **ab** (10)	0.6 ± 0.27 **b** (6)	3.0 ± 0.56 **a** (12)	1.5 ± 0.71 **ab** (22)	1.5 ± 0.71 **ab** (6)	1.5 ± 0.53 **ab** (6)	1.4 ± 0.3 **ab** (93)
Next tree (m)	2.4 ± 0.71 (13)	1.92 ± 0.32 (7)	2.8 ± 0.42 (11)	2.0 ± 0.22 (24)	1.6 ± 0.31 (6)	1.8 ± 0.52 (6)	1.6 ± 0.16 (95)
Dry edge dist (m)	8.0 ± 3.89 (15)	16.5 ± 4.17 (9)	18.0 ± 2.63 (13)	9.0 ± 1.8 (25)	16.0 ± 4.04 (6)	16.5 ± 2.84 (6)	15.3 ± 1.01 (110)
Water dist (m)	180.0 ± 63.6 (15)	150.0 ± 63.9 (9)	80.0 ± 44.0 (13)	175.0 ± 58.5 (24)	203.3 ± 93.9 (6)	37.0 ± 48.7 (6)	21.0 ± 23.8 (107)

[a] ANOVA or Kruskal-Wallis tests, * $P < 0.05$, ** $P < 0.01$
[b] Values sharing the same letter within rows do not differ significantly (see text for details of post-hoc tests used; $P > 0.05$)

APPENDIX I cont.

b) 2001:

Characteristic[a]	Northern Flicker Mean ± SE[b] (n)	Mountain Bluebird Mean ± SE (n)	Tree Swallow Mean ± SE (n)	European Starling Mean ± SE (n)	Mountain Chickadee Mean ± SE (n)	Red Squirrel Mean ± SE (n)	Unused Mean ± SE (n)
Cavity height (m) **	1.7 ± 0.18 **a** (13)	1.8 ± 0.28 **ab** (9)	2.6 ± 0.29 **ab** (10)	2.8 ± 0.22 **b** (20)	-	-	2.8 ± 0.12 **b** (116)
Vert. depth (cm) **	43.8 ± 3.31 **a** (13)	17.6 ± 3.05 **bc** (5)	15.0 ± 2.00 **b** (9)	24.4 ± 1.64 **c** (20)	-	-	27.4 ± 2.94 **bc** (92)
Horiz. depth (cm) **	16.1 ± 0.89 **ab** (13)	17.2 ± 0.94 **ab** (9)	13.7 ± 1.59 **ab** (10)	19.2 ± 1.57 **a** (20)	-	-	12.6 ± 0.51 **b** (97)
Ent. area (cm^2) **	35.7 ± 2.45 **a** (13)	31.5 ± 3.51 **ab** (9)	28.7 ± 5.53 **ab** (10)	29.8 ± 1.98 **ab** (20)	-	-	26.6 ± 2.07 **b** (96)
DBH (cm)	37.1 ± 2.57 (13)	32.7 ± 3.15 (9)	33.4 ± 4.01 (10)	36.5 ± 2.18 (20)	-	-	31.7 ± 0.79 (116)
DCH (cm) *	33.8 ± 2.02 (13)	33.0 ± 3.27 (9)	28.2 ± 2.46 (10)	35.6 ± 2.28 (20)	-	-	29.7 ± 0.90 (96)
Tree ht (m)	8.0 ± 1.34 (13)	7.8 ± 1.48 (9)	10.3 ± 1.38 (10)	9.9 ± 0.80 (20)	-	-	9.2 ± 0.41 (116)
Crown ratio	0.6 ± 0.05 (7)	0.5 ± 0.11 (5)	0.5 ± 0.07 (7)	0.5 ± 0.04 (14)	-	-	0.6 ± 0.02 (55)
Obstruction dist (m)	2.8 ± 0.98 (10)	2.1 ± 0.62 (8)	3.2 ± 0.64 (9)	3.6 ± 0.96 (17)	-	-	2.5 ± 0.27 (105)
Next tree (m) *	2.4 ± 0.36 (12)	1.8 ± 0.41 (8)	2.8 ± 0.50 (9)	4.9 ± 2.39 (20)	-	-	2.0 ± 0.16 (109)
Dry edge dist (m) *	9.2 ± 1.94 **ab** (13)	12.6 ± 2.97 **ab** (9)	15.6 ± 3.29 **ab** (10)	7.9 ± 1.58 **a** (20)	-	-	15.5 ± 1.04 **b** (116)
Water dist (m)	182.8 ± 59.3 (13)	355.6 ± 85.8 (9)	158.8 ± 65.8 (10)	307.2 ± 62.1 (20)	-	-	191.0 ± 24.5 (116)

[a] ANOVA or Kruskal-Wallis tests, * $P < 0.05$, ** $P < 0.01$

[b] Values sharing the same letter within rows do not differ significantly (see text for details of post-hoc tests used; $P > 0.5$)