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NEST SITES AND NEST WEBS FOR CAVITY-NESTING COMMUNITIES IN INTERIOR BRITISH COLUMBIA, CANADA: NEST CHARACTERISTICS AND NICHE PARTITIONING

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Abstract. The mixed forests of interior British Columbia, Canada, support a rich community of cavity nesters, accounting for about one-third of forest vertebrate species. For 20 cavity-nesting bird and six cavity-nesting mammal species, representing excavators and secondary cavity nesters, we measured nest-cavity and nest-tree characteristics over 8 years in Interior Douglas-fir (*Pseudotsuga menziesii*) forest ecosystems. There was overwhelming selection for quaking aspen (*Populus tremuloides*); 95% of 1692 cavity nests were in aspen, which comprised only 15% of trees available. The full range of live and dead trees were used, but we observed a strong preference for live trees with decay (45% of nests) or dead trees (45% of nests). A cluster analysis based on tree and cavity characteristics divided the community into five groups, including large- and medium-sized woodpeckers and a group comprised mostly of weak excavators. A fourth group included Northern Flickers (*Colaptes auratus*), the most abundant excavator, and the larger secondary cavity nesters. The final group contained the most aggressive and most abundant secondary cavity nesters. European Starling (*Sturnus vulgaris*), the most aggressive secondary cavity nester, occupied a narrower nest niche (in less-decayed trees with smaller entrances) relative to their size. Less-competitive excavators and secondary cavity nesters occupied wider nest niches in terms of tree decay class and cavity size. We constructed a nest web for community structure that showed most cavity resource use flowed up the community through aspen trees and cavities excavated by Northern Flickers. Thus, aspen was the critical nesting tree and Northern Flickers were the keystone excavators in this community.

Key words: *cavity-nesting vertebrates, community structure, keystone excavators, natural cavities, niche breadth, tree decay class.*

Sitios de Nidificación y Redes de Nidos en Comunidades que Nidifican en Cavidades en el Interior de British Columbia, Canadá: Características de los Nidos y Separación de Nichos

Resumen. Los bosques mixtos del interior de British Columbia, Canadá, albergan una rica comunidad de animales que nidifican en cavidades, los cuales representan aproximadamente un tercio de las especies de vertebrados de bosque. En este estudio medimos características de las cavidades y de los árboles de nidificación para 20 especies de aves y seis de mamíferos que nidifican en cavidades (incluyendo especies excavadoras y las que utilizan cavidades secundariamente) a lo largo de ocho años en ecosistemas de bosque interior de *Pseudotsuga menziesii*. Hubo una selección abrumadora de árboles de la especie *Populus tremuloides*; el 95% de 1692 cavidades de nidificación se encontraron en árboles de esta especie, la cual comprendía sólo el 15% de los árboles disponibles. Todo el espectro de árboles vivos y muertos fue utilizado, pero observamos una preferencia fuerte por árboles vivos con descomposición (45% de los nidos) o árboles muertos (45% de los nidos). Un análisis de agrupamiento basado en características de los árboles y las cavidades dividió la comunidad en cinco grupos, incluyendo carpinteros de tamaño grande y mediano, y un grupo formado principalmente por excavadores débiles. Un cuarto grupo incluyó al carpintero *Colaptes auratus* (el excavador más abundante) y a las especies de mayor tamaño que nidifican en cavidades secundarias. El último grupo incluyó a las especies más abundantes y agresivas que nidifican en cavidades secundarias. El estornino *Sturnus vulgaris*, la especie más agresiva que nidifica en cavidades secundarias, ocupó un nicho más estrecho (árboles menos descompuestos con entradas más pequeñas) con relación a su tamaño. Los excavadores menos competitivos y los usuarios de cavidades secundarias ocuparon nichos de ni-

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dificación más amplios en términos de la categoría de descomposición de los árboles y el tamaño de la cavidad. Construimos una red de nidos para estudiar la estructura de la comunidad, la cual mostró que la mayor parte del uso de las cavidades como recurso fluye en la comunidad a través de los árboles de *P. tremuloides* y las cavidades excavadas por *C. auratus*. Por lo tanto, *P. tremuloides* fue el árbol de nidificación crítico y *C. auratus* fue la especie de excavador clave en esta comunidad.

INTRODUCTION

Animals live in complex associations within their communities, with structure and function imposed by resource availability and by inter- and intraspecific interactions such as predation and competition (Krebs 1994). Keystone species are those that, relative to their abundance, exert disproportionate influence on the structure and function of their community (Paine 1969). Shelter-using communities, such as cavity-nesting vertebrates, may show a keystone species-driven pattern of community organization if one or a few key excavators influence species richness or abundance in the community (Martin and Eadie 1999). Thus, an excavator species may function as keystone or ecosystem architect, if it provides a critical resource in the community, such as cavities for obligate and facultative hole-nesting vertebrates.

Cavity-nesting vertebrates comprise a major component of many forest communities. About 25–30% of forest vertebrate species in the Pacific Northwest nest or roost in cavities, and most are obligate hole-nesters (Bunnell et al. 1999). Cavity-nesting species in forest ecosystems constitute a structured community that interacts through the creation of, and competition for, nest sites. Species may be classified into three guilds according to their mode of cavity acquisition. Woodpeckers, or primary cavity excavators, create holes in trees for nesting and roosting. Secondary cavity nesters, include a variety of passerines, ducks, birds of prey, and small mammals that require but cannot excavate cavities. Thus, they rely on those shelters created by excavators or a limited number of naturally occurring holes. A third guild, weak cavity excavators, may excavate their own cavities in decayed trees, use naturally occurring holes, or use cavities created by other species. The interdependence among the three groups with respect to the creation and use of nest-cavity resources has been termed a nest web (Martin and Eadie 1999). Analogous to food webs (Pimm 1980), some species depend partly or entirely on primary cavity excavators to produce a critical resource (cavities). Thus, cavity-nesting communities exhibit a hierarchical structure with potentially strong interdependencies among community members. These ecological dependencies may vary with habitat features such as forest type or tree condition.

Suitable nest cavities are essential for reproduction in most cavity-nesting species and may limit population size, especially in heavily managed landscapes (Scott 1979, Newton 1994, Holt and Martin 1997). This is especially true for secondary cavity nesters and weak excavators. For these groups, nest sites, and hence, breeding opportunities may be limited and unpredictable (Newton 1994). The extent of nest-site limitation for secondary cavity nesters depends on numbers of cavities available (natural and excavated) in relation to demand for these resources. Cavity availability may be influenced by rates of cavity creation and loss, as well as by territoriality and competition among cavity nesters. Thus, nest-site selection by secondary cavity nesters should be influenced by the number and quality of cavities available, inter- and intraspecific competition for nest sites, levels of nest depredation and parasitism, and possibly other factors.

Species using common resources may avoid interspecific competition by narrowing the niche they use, or by shifting to a portion of their niche that minimizes overlap with other species (Colwell and Fuentes 1975). Less competitive species may be required to extend their niche breadth to include less than optimal conditions, and in some cases, may opt for a bimodal distribution of resource use (e.g., pattern of resource use differs with tree species). Although some studies of cavity nesters have reported differences among species in resource use (tree preference, cavity size and orientation; van Balen et al. 1982, Li and Martin 1991), few have considered the community of cavity nesters as an integrated whole (but see Raphael and White 1984, Dobkin et al. 1995).

Patterns of tree and cavity occupancy are central to understanding the population ecology of cavity-nesting species. In this study, we describe nest-site use in relation to availability for 26 species in three guilds, and examine degrees of overlap in nest-site use among species. Because quaking aspen (*Populus tremuloides*) was strongly preferred for excavation over conifers, we examined use by cavity nesters of aspen tree size and decay class in relation to availability. We predicted that resource partitioning should be better developed among excavators because they have the ability to create cavities that match their body size, but they must be able to access trees of appropriate size and condition to match their excavation abilities. Secondary cavity nesters should show considerably more resource overlap as they are expected to have less choice in a regime of competition for optimal nest-site types or context. We conducted a cluster analysis to examine niche overlap in tree and cavity characteristics within and across guilds, and secondarily examined potential for cavity-nester body size to further increase niche partitioning. Differential competitive abilities might reduce resource-use overlap of secondary cavity nesters if aggressive species use a narrow niche of favored cavities (specialists) and less competitive species become generalist cavity users by necessity.

METHODS

STUDY AREA

Between 1995 and 2002, we located cavities and monitored nests of cavity-nesting birds and mammals on our study area in the Cariboo-Chilcotin region of central interior British Columbia, Canada (51°52′N, 122°21′W). In 1995, we established 11 sampling sites, increased to 16 sites in 1996, and since 1998 have monitored 28 sites. The study area was composed of mixed coniferous and deciduous forest embedded in a matrix of grassland and shallow ponds within the warm and dry Interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). Predominant tree species were quaking aspen, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* and *P. glauca* × *engelmannii*). Twenty-six sampling sites were mature forest (80–200 years old), nine of which were selectively cut for pine or spruce in 1997–2002. Two sites were selectively logged for Douglas-fir in the 1940s. Our sampling sites (7–32 ha in size) varied in character from continuous forest to two sites that were a series of ‘‘forest islands’’ (0.2 to 5 ha) within a grassland matrix. Additional details for study area and project design are given in Martin and Eadie (1999), and Aitken et al. (2002).

NEST LOCATION AND MONITORING

The cavity-nesting community in the area consisted of 31 bird and 12 mammal species (Martin and Eadie 1999). From 1 May to 31 July, we searched for all occupied cavity nests on our sites. Given the northern latitude of our study area, most migratory and resident cavity nesters did not begin nesting until the first or second week of May. Our goal was to determine the extent of use by cavity nesters across a range of forest stand types, and not to maximize the number of nests for any single species. Thus we conducted systematic nest searches across all sites for an average of 6–7 observer-hr of nest searching per sampling site per week. In this paper, we also included nest characteristics data (in Tables 1 and 2) for nests located away from our established sampling sites for uncommon species or those with large home ranges. Because cavity nesters reused cavities and nest trees in multiple years (Aitken et al. 2002), we checked existing cavities (both previously used and those not known to be occupied in previous years), as well as searching for newly excavated cavities.

Occupied cavities were located by looking or listening for excavation, by tapping or scraping at the base of trees containing cavities to detect occupants, and by observing breeding birds or hearing begging nestlings. Finding occupied nests was facilitated by detecting cavity nesters during early morning point-count surveys. Cavities within reach of a ladder (≤5.2 m) were inspected visually with flashlights and mirrors to establish clutch size, nesting stage, status, and fate where possible. Nests were considered occupied if they contained at least one egg or nestling. We also monitored cavities occupied by cavity-nesting mammals such as red squirrel, northern flying squirrel, and bushy-tailed woodrat. In Tables 1 and 2, we also report occasional use by facultative cavity users such as chipmunk, deer mouse, and short-tailed weasel. Occupied cavities were assigned unique numbers and nest trees were marked with numbered aluminum tags to facilitate relocation. We classified Mountain Chickadees as secondary cavity nesters as per Hill and Lein (1988).

TABLE 1. Tree species and decay class of nests occupied by cavity nesters in interior British Columbia, 1995–2002. Dbh = diameter at breast height; *n* is the number of occupied nests. Decay class follows Thomas et al. 1979, with no occupied nests in decay class 8 and a total of 17 nests (15 of these in aspen) in fallen trees (decay classes 10 and 11).

	Quaking aspen			Douglas-fir		
Species	Dbh mean ± SD	Decay median (range)	*n*	Dbh mean ± SD	Decay median (range)	*n*
Primary cavity excavators						
Red-naped Sapsucker	31.2 ± 6.7	2 (1–4)	193			
Hairy Woodpecker	30.3 ± 5.0	2 (1–3)	33			
American Three-toed Woodpecker	23.7 ± 4.1	2 (2–5)	15			
Black-backed Woodpecker						
Northern Flicker	34.7 ± 8.8	3 (1–6)	227	92.1 ± 11.3	2 (2–3)	3
Pileated Woodpecker	44.8 ± 3.4	2 (1–4)	18			
Weak cavity excavators						
Downy Woodpecker	25.1 ± 6.2	3 (2–5)	26			
Black-capped Chickadee	20.4 ± 7.8	3 (1–7)	35			
Red-breasted Nuthatch[a]	23.2 ± 7.6	3 (1–10)	149	70.3 ± 33.4	4 (3–5)	6
Secondary cavity nesters						
Wood Duck	45.4	2	1			
Bufflehead[b]	33.3 ± 9.6	3 (2–6)	31	82.9 ± 22.7	3.5 (2–5)	2
Barrow's Goldeneye	48.2 ± 3.8	2 (2–4)	3			
Hooded Merganser[a]	42.7	2	1			
American Kestrel	40.7 ± 8.5	3 (2–5)	23			
Northern Hawk Owl[b]	41.3	4	2			
Northern Saw-whet Owl	38.1 ± 9.3	3.5 (1–4)	10			
Tree Swallow	29.2 ± 7.3	2 (1–6)	183	95.0	11	1
Mountain Chickadee	24.9 ± 7.0	3 (1–6)	207	42.3 ± 14.0	4 (4–5)	4
Mountain Bluebird	31.3 ± 10.2	3 (1–10)	127	125.0	11	1
European Starling	35.0 ± 8.5	2 (1–10)	263	98.4	2	1
Northern flying squirrel	29.3 ± 4.5	3 (1–5)	13			
Bushy-tailed woodrat	28.4 ± 11.3	4 (4)	3			
Red squirrel	29.3 ± 8.7	2 (1–6)	45	37.9	2	1
Chipmunk	13.0	10 (10)	2			
Short-tailed weasel	25.2	4	1			
Deer mouse	36.0	5	1			
All cavity-nesting species	30.5 ± 9.2	2 (1–10)	1612	74.8 ± 30.6	4 (2–11)	19
Bark nesters						
Brown Creeper						

[a] One Hooded Merganser nest and two Red-breasted Nuthatch nests were in cottonwood (*Populus trichocarpa*) trees.
[b] Two nesting attempts in sequential years in same cavity.

NEST-TREE AND CAVITY CHARACTERISTICS

After nest cavities were vacated, we recorded tree and cavity variables. Tree characteristics included species, diameter at breast height (dbh), and decay class. We used a tree decay classification system that ranged from 1–8 for standing trees, with 1 indicating a live tree with no visible signs of decay, 2 indicating a live tree with visible signs of decay, and 3–8 indicating dead trees with advancing stages of decay (Thomas et al. 1979, see Fig. 1C for decay class icons). Tree condition was assessed using British Columbia Ministry of Forests guidelines (Finck et al. 1989) and included the presence of fungal conks, bark beetle sign, and broken top. We included only standing trees in our analyses, but for completeness, we report all occupied cavities in Table 1 (1% of occupied nests were found in downed trees; 15 nests in trees that had fallen over naturally [decay class 10] and two nests in trees that were cut down [decay class 11]). Cavity variables included the observed or probable excavator species (when we had reasonable certainty), height of cavity in tree (m), and vertical

TABLE 1. Extended.

Lodgepole pine			Hybrid spruce			All tree species		
Dbh mean ± SD	Decay median (range)	*n*	Dbh mean ± SD	Decay median (range)	*n*	Dbh mean ± SD	Decay median (range)	*n*
						31.2 ± 6.7	2 (1–4)	193
						30.3 ± 5.0	2 (1–3)	33
26.6 ± 3.6	2 (1–3)	2	35.9 ± 13.5	4 (3–4)	3	25.8 ± 7.2	2.5 (1–5)	20
30.9 ± 2.5	2 (2)	2				30.9 ± 2.6	2 (2)	2
32.9 ± 8.5	2 (2–5)	6				35.4 ± 10.9	3 (1–6)	236
						44.8 ± 3.4	2 (1–4)	18
						25.1 ± 6.2	3 (2–5)	26
						20.4 ± 7.8	3 (1–7)	35
27.0 ± 11.6	3 (3–4)	5	32.5 ± 9.0	3.5 (3–4)	4	25.7 ± 13.5	3 (1–10)	166
						45.4	2	1
42.5	2 (2)	2				36.6 ± 15.3	3 (2–6)	35
						48.2 ± 3.8	2 (2–4)	3
						49.4 ± 9.6	1.5 (2–4)	2
40.9 ± 1.5	2 (2–5)	3				40.7 ± 8.0	3 (2–5)	26
						41.3	4 (4)	2
						38.1 ± 9.3	3.5 (1–4)	10
26.7 ± 4.4	6 (1–6)	5		3.5 (3–4)	2	29.4 ± 8.7	2 (1–11)	191
19.9	1	1				25.2 ± 7.4	3 (1–6)	212
41.9 ± 5.7	2.5 (1–6)	14				33.0 ± 12.9	3 (1–11)	142
40.1 ± 1.9	2 (1–2)	3				35.3 ± 9.3	2 (1–10)	267
31.5	3	1				29.5 ± 4.4	3 (1–5)	14
						28.4 ± 11.3	4 (4)	3
38.7 ± 10.7	3 (2–6)	4		4 (4)	1	30.3 ± 9.0	2 (1–6)	51
						13.0	10 (10)	2
						25.2	4	1
						36.0	5	1
35.3 ± 9.1	4 (1–6)	48	34.0 ± 9.5	4 (3–4)	10	31.2 ± 10.8	2 (1–11)	1692
30.9 ± 3.1	4 (4–5)	3				30.9 ± 3.1	4 (4–5)	3

cavity depth, internal cavity diameter, entrance hole height, and width (cm). Vertical cavity depth was measured from the bottom of the cavity entrance to the bottom of the cavity. Internal cavity diameter was measured from the inner edge of the lower lip of the entrance to the back wall of the cavity. Entrance hole area (cm^2) was calculated using hole height and width and the formula for the area of an ellipse. Cavity volume (cm^3) was calculated using vertical depth and internal cavity diameter and the formula for the volume of a cylinder.

To examine tree species and characteristics available in the landscape, we measured trees and cavities in 11.2-m-radius circular plots around each nest tree and at point-count stations 100 m apart along transect lines that had been established throughout each sampling site. On continuous forest sites, transects were spaced systematically in a 100 $\times$ 100 m grid starting at a grassland or wetland edge and extending 500 m into the forest. On sampling sites with forest islands where it was not possible to establish a grid, we placed vegetation plots at least 100 m apart. Most sites covered an area that included one or several territories of most cavity-nesting species present, and thus the habitat characteristics averaged over all vegetation plots on a

TABLE 2. Cavity nest-site characteristics for birds and mammals in interior British Columbia, 1995–2002. *n* is the number of measured cavities.

Species	Height above ground (m)		Vertical depth (cm)		Internal cavity diameter (cm)		Entrance area (cm^2)		Number of cavities in tree	
	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*
Primary cavity excavators										
Red-naped Sapsucker	6.1 ± 2.8	193	18.6 ± 4.9	62	10.0 ± 2.3	72	12.5 ± 2.9	70	2.4 ± 2.0	187
Hairy Woodpecker	6.2 ± 2.1	33	23.9 ± 2.8	10	11.7 ± 1.0	10	21.3 ± 4.3	11	1.4 ± 0.8	32
American Three-toed Woodpecker	4.2 ± 2.2	21	18.4 ± 2.9	13	12.5 ± 4.6	13	16.1 ± 5.6	13	1.3 ± 0.4	20
Black-backed Woodpecker	6.1 ± 2.2	2	15.5	1	11.2	1	18.1	1	1.0 ± 0.0	2
Northern Flicker	3.5 ± 2.4	238	38.9 ± 15.5	151	16.2 ± 4.4	160	35.6 ± 9.4	159	2.0 ± 1.6	227
Pileated Woodpecker	9.7 ± 2.8	18	37	1	18.7	1	69.1	1	2.1 ± 1.5	17
Weak cavity excavators										
Downy Woodpecker	6.0 ± 3.2	26	16.9 ± 4.7	8	9.1 ± 1.2	8	9.1 ± 2.6	8	2.3 ± 2.1	26
Black-capped Chickadee	4.2 ± 2.6	35	13.9 ± 4.3	13	6.9 ± 2.2	15	12.1 ± 5.9	14	1.3 ± 0.7	35
Red-breasted Nuthatch	5.4 ± 3.2	165	10.9 ± 3.2	45	7.2 ± 2.5	58	9.0 ± 5.1	60	1.8 ± 1.7	164
Secondary cavity nesters										
Wood Duck	7.5	1							1	1
Bufflehead	4.7 ± 1.7	35	31.9 ± 22.0	14	18.0 ± 5.9	15	33.4 ± 7.4	13	2.4 ± 1.7	35
Barrow's Goldeneye	6.1 ± 2.5	3	26.0	1	19.0	1	33.0	1	3.0 ± 2.8	2
Hooded Merganser	4.1	1	43.0	1	20.1	1			6	1
American Kestrel	3.3 ± 2.3	26	33.4 ± 6.8	16	15.2 ± 3.6	18	38.0 ± 17.4	18	2.0 ± 1.4	24
Northern Hawk Owl	4.5	1	21.5 ± 2.1	2	25.5	1			1.0 ± 0.0	2
Northern Saw-whet Owl	6.0 ± 4.0	10	22.8 ± 7.3	5	13.9 ± 2.7	5	32.4 ± 7.4	5	2.6 ± 1.6	10
Tree Swallow	4.3 ± 2.5	190	15.1 ± 8.2	92	11.5 ± 4.2	107	26.7 ± 18.5	109	2.5 ± 2.5	185
Mountain Chickadee	4.9 ± 2.8	211	12.9 ± 7.2	104	9.5 ± 3.3	109	12.9 ± 7.3	114	2.5 ± 2.3	210
Mountain Bluebird	2.8 ± 2.4	143	17.1 ± 9.9	94	13.7 ± 7.4	120	32.7 ± 17.9	120	1.7 ± 1.1	139
European Starling	3.9 ± 2.2	267	24.7 ± 10.8	151	16.0 ± 6.0	156	30.1 ± 9.9	158	1.8 ± 1.5	257
Northern flying squirrel	3.8 ± 3.7	14	15.3 ± 9.2	8	13.9 ± 2.5	11	28.8 ± 30.9	11	1.9 ± 1.4	14
Bushy-tailed woodrat	1.7 ± 0.4	3	20.2 ± 12.4	2	16.2 ± 4.0	2	47.4 ± 41.2	2	1.7 ± 1.2	3
Red squirrel	3.7 ± 2.1	51	20.4 ± 26.1	26	13.1 ± 4.7	30	21.2 ± 16.3	38	2.2 ± 1.5	49
Chipmunk	0.0 ± 0.0	2			35.0	1	75.0 ± 33.9	2	1.0 ± 0.0	2
Short-tailed weasel	5.0	1							6	1
Deer mouse	1.3	1			21.5	1	29.2	1	1	1
All cavity-nesting species	4.5 ± 2.8	1690	22.4 ± 14.6	820	13.0 ± 5.7	916	25.4 ± 15.8	930	2.1 ± 1.8	1646
Bark nesters										
Brown Creeper	2.2 ± 0.9	3							0.3 ± 0.6	3

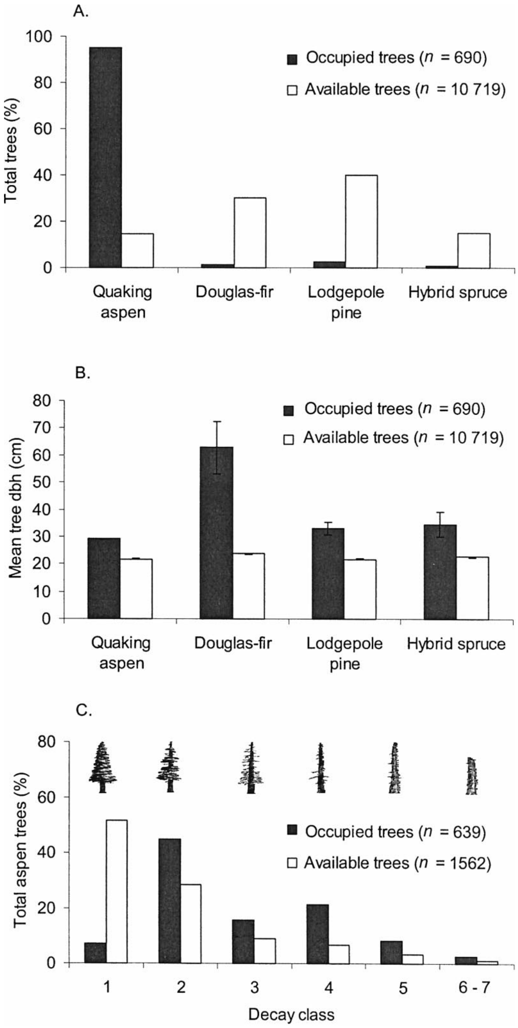

FIGURE 1. Selection of tree species and nest-tree characteristics by cavity-nesting birds in relation to availability in interior British Columbia. (A) Tree species, (B) diameter at breast height (dbh), and (C) decay class. Icons in (C) illustrate general differences between decay classes (Thomas et al. 1979). Each occupied or available tree was included only once, although multiple cavities may have been occupied in a tree or individual cavities occupied multiple times. Occupied trees refer to the sample of nest trees that included only the most recent nesting attempt, and available trees were the most complete and recent set of vegetation plot data.

sampling site represented availability of nesting resources with a sampling effort of approximately one vegetation plot ha^{-1}. Within an 11.2-m radius for both nest plots and systematically selected point-count stations on sampling sites, we recorded for all trees ≥12.5 cm dbh (British Columbia Ministry of Forests inventory standard) tree species, size (dbh), decay class, and the number of cavities (used or unused) present.

STATISTICAL ANALYSES

Except where indicated (e.g., resource selection at the tree level, Fig. 1), we counted every nesting attempt as an independent data point, including cases where a cavity was used more than once in a season and in more than one year, because we wanted a general picture of the nesting niches for each species. There were 28 cases of within-season cavity reuse by individuals of two different species, and 30 cases of within-season reuse by individuals of the same species. For all cavity and tree characteristics, excluding decay class, we present means and report standard deviations (SD). Decay class was treated as a rank variable and we present the range of values. Due to small sample sizes, decay classes 6 ($n = 25$ occupied nests) and 7 ($n = 3$ nests) were pooled in analyses.

Data were analyzed using SPSS for Windows version 10.0.7 (SPSS Inc. 2000). Statistical tests were two-tailed and significance levels of $\alpha = 0.05$ were used. Continuous variables were tested for normality using a one-sample Kolmogorov-Smirnov test at the 95% confidence level (Zar 1999). Where possible, non-normally distributed variables were $\log_{10}$ transformed. Homoscedasticity was tested using Levene's test for homogeneity of variance. One-way ANOVA was used to compare normally distributed or $\log_{10}$ transformed tree and nest cavity characteristics among species with more than 10 nests. We used nonparametric Kruskal-Wallis tests where transformations failed to meet parametric assumptions (Zar 1999).

Cluster analysis (using average linkage between groups; SPSS Inc. 2000) was used to group species with $n \geq 10$ nests on the basis of similarities in nest cavity and tree characteristics (cavity height above ground, vertical depth, internal diameter, entrance area, and tree dbh). To examine how cavity-nester body size might explain further niche partitioning of cavity size, we used mean mass of species using data from breeding birds captured on our sites (10 species) or from the literature, and regressed estimated body mass against entrance hole size and cavity volume. Where only females enter cavities (e.g., Bufflehead) we used mean female mass.

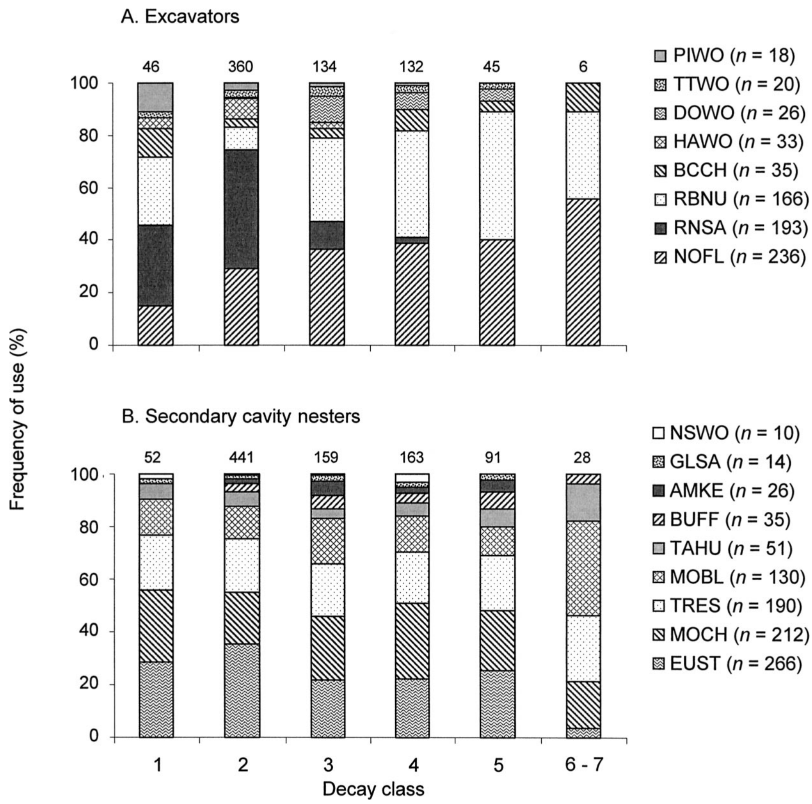

FIGURE 2. Proportion of (A) cavity excavators and (B) secondary cavity nesters using trees in decay class 1–7 (Thomas et al. 1979) for nesting. See Appendix for bird codes. Numbers above bars indicate the total sample of occupied nests for each decay class. No birds nested in decay class 8.

RESULTS

NEST-TREE AND CAVITY CHARACTERISTICS

We located and tagged a total of 1692 occupied cavity nests representing 20 species of birds and six species of small mammals from 1995 to 2002 (Table 1; scientific names appear in Appendix). We included nest data for Brown Creeper, which are bark nesters, and facultative cavity-nesting mammals (e.g., chipmunks), as other studies often include them with cavity nesters, and forestry activities may also alter nest-site availability for them. Over 95% of nests were in quaking aspen, 3% were in lodgepole pine, 1% in Douglas-fir, and 0.6% in spruce, consistent with results reported earlier with a sample of 201 nests (Martin and Eadie 1999). There was strong selection for cavities in aspen across all guilds and all species (Fig. 1A). Among excavators that used aspen, American Three-toed Woodpeckers used it the least, but still selected aspen for 75% of their nests. Among the secondary cavity nesters (with >15 nests), red squirrels were least likely to nest in aspen (88% of nests; Table 1).

Cavity nesters selected larger trees for nesting relative to what was available for the four most abundant tree species on our sampling sites, with the most pronounced selection for large Douglas-fir trees (Fig. 1B). Mean nest-tree dbh differed significantly among cavity nester species ($F_{16, 1646} = 34.4$, $P < 0.001$; Table 1). Downy Woodpeckers, Black-capped Chickadees, Mountain Chickadees, and Red-breasted Nuthatches used the smallest diameter trees, while Pileated Woodpeckers used the largest trees. On our sites, cavity nesters selected trees across a wide range of decay classes for nesting (although trees in decay class 8 were not used by any species), but showed the strongest selection for live trees with onset of decay (decay class 2) and dead trees (3–6; Fig. 1C). Trees in each decay class were used by a surprising range of excavators and

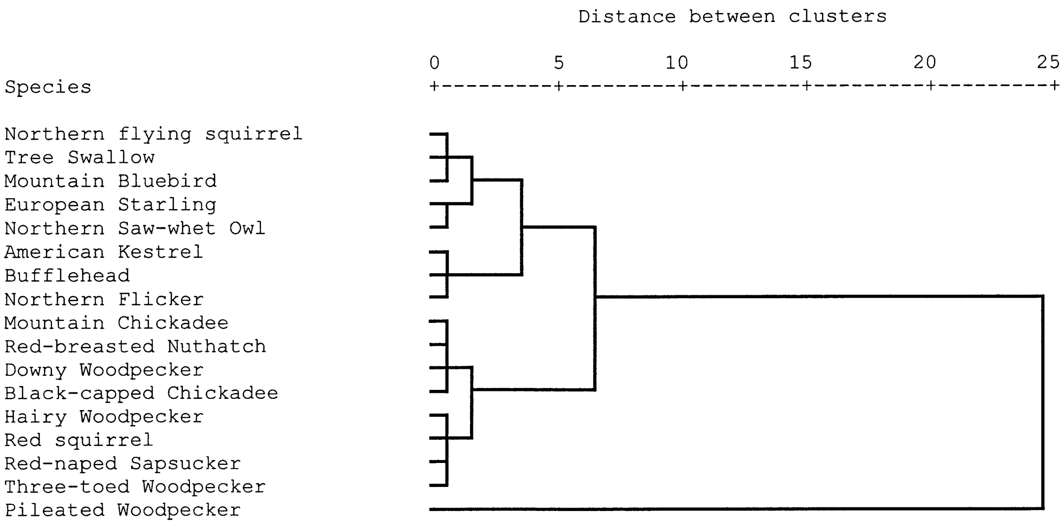

FIGURE 3. Dendrogram showing results of a cluster analysis used to group cavity-nesting species on the basis of similarities for nest-tree size (dbh) and cavity characteristics (cavity height above ground, hole entrance area, vertical depth, and internal diameter). The least similar clusters have the greatest distance between separating branches. Analysis included all species with ≥10 nests, for a total of 1676 nests; data are in Tables 1 and 2.

secondary cavity nesters, with the greatest diversity of species using decay classes 2 to 4 (15–16 species for each class; Fig. 2). As expected, a greater range of excavator species used trees in the lower decay classes. Flickers, nuthatches, and Black-capped Chickadees used the full range of decay classes for nesting; the latter two species often excavated in dead branches of live trees (Fig. 2A). Pileated Woodpeckers, Hairy Woodpeckers, and Red-naped Sapsuckers primarily used live trees, while Downy Woodpeckers selected trees with advanced decay. As predicted, secondary cavity nesters showed considerable overlap in nest-tree decay classes (Fig. 2B). Interestingly, all five species with ≥50 nests used the full range of tree decay classes. However, European Starlings, the most aggressive secondary cavity nester species, occupied generally more robust trees (i.e., lower decay classes). About 64% of starling nests were in decay class 1 and 2 trees, while the other species ranged from 47–53%.

As expected, cavity height above ground, vertical depth, internal diameter, and entrance area varied significantly across species (Table 2; cavity height: Kruskal-Wallis $\chi^2_{15} = 271.0$, $P < 0.001$; vertical depth: $F_{15,\ 795} = 39.7$, $P < 0.001$; internal diameter: $\chi^2_{15} = 390.4$, $P < 0.001$; entrance area: $\chi^2_{15} = 501.2$, $P < 0.001$). Downy Woodpeckers, Black-capped and Mountain Chickadees, and Red-breasted Nuthatches used the smallest cavities (as calculated using internal cavity diameter in Table 2), while Buffleheads, flickers, and American Kestrels used the largest holes. Bluebird nests were lowest (mean <3 m above ground), while Pileated Woodpecker cavities were highest, averaging nearly 10 m above ground.

Cluster analysis of cavity height above ground, vertical depth, internal diameter, entrance area, and dbh produced five species groupings (Fig. 3). The first branch of the dendrogram contained just one species, Pileated Woodpecker, which had the greatest separation from and least similarity to the other species. The second group included four secondary cavity-nesting birds (Tree Swallow, Mountain Bluebird, European Starling, Northern Saw-whet Owl), and one small mammal (northern flying squirrel). The third group included one excavator (Northern Flicker) and two secondary cavity nesters (American Kestrel and Bufflehead). The fourth group consisted of the four smallest species, and included all three weak excavators (Downy Woodpecker, Black-capped Chickadee, and Red-breasted Nuthatch), as well as Mountain Chickadee. The final group included three medium-sized woodpeckers (Red-naped Sapsucker, Hairy Woodpecker, and American Three-

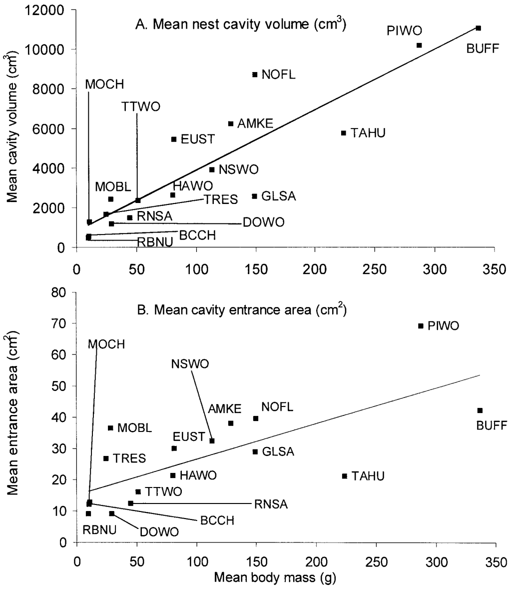

FIGURE 4. Preliminary examination of cavity size–body size relationships for cavity-nesting birds and mammals, showing significant positive relationships between mean body mass (g) and (A) mean nest cavity volume (cm^3) and (B) mean cavity entrance area (cm^2). See Appendix for four-letter species codes.

toed Woodpecker), and red squirrel, the most abundant cavity-nesting small mammal.

Body size of cavity nesters is a major component determining the degree of resource overlap in cavity nests. As a preliminary examination of body size–cavity size relationships, we regressed two aspects of cavity size against mean body mass of cavity-nesters (a surrogate for body size). We found overall strong positive relationships with body mass (g) and cavity volume (cm^3; $r^2 = 0.82$, $F_{1,15} = 69.2$, $P < 0.001$), as well as with hole entrance area (cm^2; $r^2 = 0.53$, $F_{1,15} = 17.1$, $P < 0.001$; Fig. 4). Mountain Bluebirds and Tree Swallows occupied cavities with volumes expected for their body size, but the hole entrance area was considerably larger relative to other species weighing less than 50 g.

Integrating tree and cavity characteristics across the community, we summarized nest-site use through the cavity-nesting vertebrate community in interior British Columbia. We found that community nest use was organized in discrete levels and was strongly structured through cavities excavated by Northern Flickers and in aspen trees (Fig. 5). Some secondary cavity nesters such as American Kestrel and European Starling used flicker-excavated cavities almost exclusively, while other species such as Tree Swallow and red squirrel used cavities from five or more excavator species. Nest-use relationships for species with fewer than 15 nests must be interpreted cautiously (i.e., for one excavator and six secondary cavity nesters in our study; Fig. 5). However, our suggested nest-use relationship for Barrow's Goldeneye was supported by a concurrent study that included our study area: most of the 39 natural cavities occupied by goldeneyes were created by Pileated Woodpeckers (Evans et al. 2002). Finally, we note that although Red-naped Sapsuckers were almost as abundant as flickers on our sites, they appeared relatively unimportant in the nest web with no secondary cavity nester specializing on using their cavities.

DISCUSSION

Elucidating the critical processes that determine community structure and function for complex communities in variable environments can be extremely challenging. Confirming the role of a keystone species is most easily achieved by removal experiments (Krebs 1994), but such experiments are often not practical or desirable until the basic patterns of resource use in relation to resource availability have been determined across a range of habitat conditions. In this paper, we described patterns of nest-site use and hierarchical organization for a cavity-nesting vertebrate community. We found strong support for a bottom-up model of community organization for cavity nesters, where nesting resources flowed up through aspen and Northern Flickers to a diverse community of secondary cavity-nesting birds and mammals. In fact, there are over 32 secondary cavity-nesting species resident in this community (Martin and Eadie 1999), but we were unable to obtain sufficient data to measure nesting resource use by bats and several raptor and waterfowl species.

NEST-TREE CHARACTERISTICS AND RESOURCE OVERLAP

In Interior Douglas-fir forests, we found cavity-nesters used the dominant deciduous tree, quaking aspen, almost exclusively. Thus, in this large community, there was little evidence of nest resource partitioning by tree species. Aspen may be the preferred tree for excavators because it is susceptible to heartwood rot, which provides a

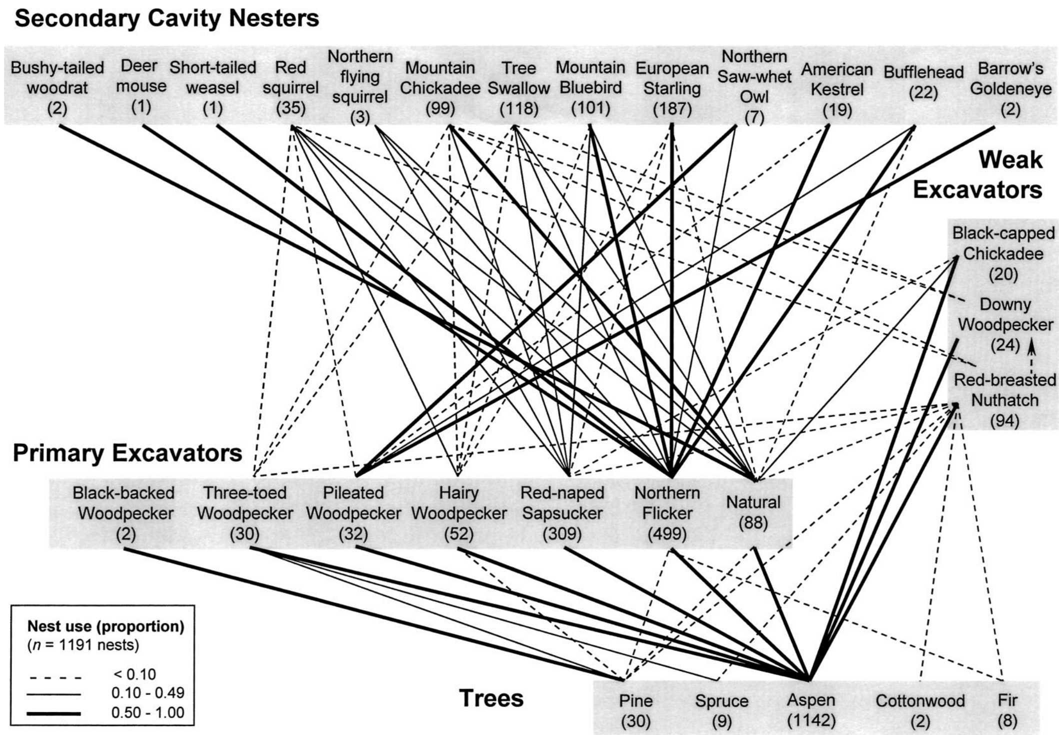

FIGURE 5. A nest web diagramming resource flow (cavity or tree) through the cavity-nesting vertebrate community in interior British Columbia. Resource use in the nest web shows links between species using nests (secondary cavity nesters and excavators) and the excavator or tree species that provided the resource. For example, Bufflehead (n = 22 nests) primarily used flicker cavities, but regularly (10–49% of cases) occupied cavities excavated by Pileated Woodpecker, and occasionally (<10%) used naturally occurring cavities. Numbers under each species indicate the number of occupied nests for which there was information on the excavator or tree species used. Links for species with fewer than 15 occupied nests are considered preliminary findings.

soft substrate for excavation while retaining a firm sapwood shell that gives stability for the cavity (Conner et al. 1976, Harestad and Keisker 1989). Aspen bark retains integrity even when trees are in advanced stages of decay, thus allowing weak excavators to create cavities. Because aspen are shorter-lived than conifers, but have sufficient structural integrity to remain standing when dead, mature forests comprise a considerable proportion of dead or decaying trees. On our sites, 45% of standing aspen were dying or dead compared to 10–15% for the three conifer species (Martin et al., unpubl. data). Thus the demography, health, and integrity of sapwood and bark make aspen the tree of choice for all excavator species on our study area.

Desired resources may be restricted even when they appear abundant. Aspen, the species in highest demand for nest trees, represented only 15% of trees on our sites. When one considers that only 45% of aspen were in the most preferred decay classes, then less than 7% of trees on our sites represented high-quality nesting trees. Trees in advanced stages of decay may be less stable and more prone to blow down than less decayed trees. Furthermore, the spatial context of nest trees such as their distance to forest edge is important in determining use of cavities, with many species showing a strong preference for nest trees close to edges (Gutzwiller and Anderson 1986, 1987, Dobkin et al. 1995, Aitken et al. 2002).

Excavators can achieve resource partitioning by selecting suitable nest trees in relation to a variety of habitat contexts, such as distance to edge or type of edge. In our study, this may have occurred between the two groups of primary excavators with overlapping tree characteristics; Red-naped Sapsuckers nested <30 m from forest edge perhaps due to foraging preferences in open habitats, whereas Hairy Woodpeckers nested >100 m from edge (Martin et al., unpubl. data). Spatial context did not allow separation for two weak excavators, Downy Woodpeckers and Red-breasted Nuthatches, which showed strong niche overlap with respect to nest-tree and cavity characteristics. Red-breasted Nuthatches occupied a broader niche than Downy Woodpeckers in terms of cavity acquisition, excavating in all five trees species in our study areas, as well as using cavities excavated by three species of woodpeckers and natural holes (Fig. 5). Possibly, nuthatches have responded to nest-site competition with Downy Woodpeckers by adopting a mixed excavator–secondary cavity nester strategy and having the widest niche breadth of any excavator.

NEST-SITE CHARACTERISTICS

We presented two types of cavity measurements, height above ground and cavity size, that relate to aspects of cavity-nester life history. Cavity height and hole entrance area can influence predation risk (Nilsson 1984), while internal cavity size may relate to fecundity and fledging success. Li and Martin (1991) found that secondary cavity nesters use cavities that are lower and more concealed than excavators. In other studies, Tree Swallows, Red-naped Sapsuckers, and Mountain Chickadees preferred higher nests, while Northern Flickers preferred lower nests (Hill and Lein 1988, Dobkin et al. 1995), and Mountain Bluebirds displayed no preference for height of nest boxes (Holt and Martin 1997).

Cavity size is an important factor in determining cavity use because it influences the array of species able to use the cavity, and because it can affect reproductive success, competition, and predation. Entrance size limits the range of species that can use a cavity (Peterson and Gauthier 1985). Smaller entrance holes are advantageous in deterring predators and in reducing the chance of eviction from the cavity by a larger competitor (Zeleny 1978, Moeed and Dawson 1979, Robertson and Rendell 1990). Peterson and Gauthier (1985) found that cavity volume and entrance size were the most important variables in determining cavity occupancy by flickers and several secondary cavity nesters. Large cavities may allow for better thermoregulation by chicks on hot days (van Balen 1984) and reduce competition for space and feeding positions among siblings (Slagsvold 1989). On our study area, mortality of flicker nestlings was lower in spacious cavities (Wiebe and Swift 2001). Cavity depth may influence predation risk, as deeper cavities can prevent mammalian predators from reaching in to remove young. Some studies have found higher rates of predation associated with larger nest boxes (Zeleny 1978), but there was no relationship between natural cavity size and predation rate for flickers in our area (Wiebe and Swift 2001). Generally, the ideal cavity to maximize fecundity and minimize depredation is a large-volume cavity with a small entrance. The optimal cavity size and volume should scale to the body size of each species, thus allowing considerable scope for niche partitioning in a diverse community of cavity nesters.

Nest excavation is assumed to be energetically costly, and there are likely both costs and benefits to excavating in decayed trees. Soft wood may allow larger cavities for a given energy expenditure but cavity soundness may alter cavity microclimate or the ability of predators to access nests. Cavities in softer decayed trees reached higher maximum temperatures and had greater daily fluctuations than those in harder wood (Wiebe 2001). Temperature fluctuations may affect egg viability, and the ability of nestlings and incubating adults to thermoregulate (White and Kinney 1974, Webb 1987), although this was not the case for flickers on our study area (Wiebe 2001). Both Black-capped and Carolina Chickadees (*Poecile carolinensis*) had higher nest success in trees with harder wood and thicker walls, which may have prevented access by predators (Albano 1992, Christman and Dhondt 1997).

INTER- AND INTRAGUILD COMPETITION AND NICHE PARTITIONING

In an earlier paper, we found strong positive relationships between detections of excavators and secondary cavity nesters across a range of stand types, with some stands being rich in both guilds, and other stands quite impoverished in both (Martin and Eadie 1999). Despite a community of nine excavator species, most secondary cavity nesters, with the exception of goldeneyes, used cavities excavated by flickers. Similar preferences for aspen and flicker-excavated holes were found for reused cavities (Aitken et al. 2002).

Our cluster analysis showed potential for niche partitioning at the community level with five separate species groupings. Pileated Woodpeckers and the large cavity-nesting ducks and raptors, the least well-represented species in our study, comprised the most discrete group. A study of ducks nesting in natural cavities that included our sampling sites found goldeneyes only used Pileated Woodpecker holes or natural holes, while Buffleheads used Pileated Woodpecker and flicker cavities about equally (M. Evans, pers. comm.). Hence, in our area, Pileated Woodpeckers were keystone excavators allowing for a reasonably diverse group of large-bodied cavity nesters.

Chickadees and nuthatches, which were grouped together in our cluster analysis, have considerable resource overlap and thus strong potential for competition. Hill and Lein (1988) suggested that sympatric Mountain and Black-capped Chickadees avoid competition by ecological segregation of nesting and foraging sites. On our study sites, the two species occupied different nesting guilds, as Black-capped Chickadees excavated and Mountain Chickadees did not. Although they have similar body mass, Mountain Chickadees (mean mass = 11.1 ± 0.8 g [SD], n = 63 birds) used significantly larger cavities than Black-capped Chickadees (11.0 ± 1.2 g, n = 10 birds, Martin et al., unpubl. data). About one-third of Mountain Chickadee nests were in holes excavated by Red-naped Sapsuckers (Aitken et al. 2002, this study). Black-capped Chickadees showed considerable variability in nest-site substrates as they excavated holes in the tops of small stumps (<1 m high) and in small crevices in the forked trunks of healthy trees. Mountain Chickadees suffered higher nest predation than Black-capped Chickadees, perhaps because they used nest sites excavated by a medium-sized woodpecker in a size grouping that also included red squirrels, a generalist predator. By nesting in larger cavities relative to their body size, Mountain Chickadees may be more vulnerable to nest predation by small mammals than Black-capped Chickadees.

The second and third groups in the cluster analysis separated according to body size, with the cluster of flicker, kestrel, and Bufflehead generally of larger body size than the starling, saw-whet owl, and flying squirrel cluster. Despite body size differences, we observed inter- and intraguild competition among these groups, which cross trophic levels as well as nest-use levels. Northern Flickers excavated cavities, but they also reused nest sites and, as secondary cavity nesters, they must compete for nests with starlings and kestrels (Ingold 1994, Sedgwick 1997, Aitken et al. 2002). Starlings are highly successful competitors and often usurp cavities from excavators, particularly flickers, and from other secondary cavity nesters, including kestrels and cavity-nesting ducks. On our study area, starlings usurped about 7% of flicker nests annually and destroyed eggs in natural cavity nests and nest boxes of Bufflehead and Barrow's Goldeneye (Evans et al. 2002, Wiebe 2003). Cavity-nesting mammals are cryptic cavity users and most studies that do not check cavities visually underestimate their importance as nest-site competitors. In interior British Columbia, red squirrels and flying squirrels regularly rear broods in cavities and fill cavities with nesting material and cones. Both squirrels prey on eggs and adult birds. Thus, even if squirrels do not occupy or fill a nest, prospecting trips into cavities in spring may deter avian secondary cavity nesters from occupying those cavities (Aitken et al. 2002, Lawler and Edwards 2002).

Much of our understanding of cavity-nester population dynamics comes from studies of one or a few species in heavily managed landscapes (Newton 1994). Community-wide studies in natural forest conditions are needed to investigate the ecological relationships and population dynamics among the members of diverse cavity-nesting communities (Martin and Eadie 1999). In our community, we have one or possibly two keystone excavators. Northern Flickers are abundant woodpeckers that create large holes, and thus are likely responsible for the diverse and abundant array of secondary cavity-nesting vertebrates. Pileated Woodpeckers are less abundant, but add important complexity to the cavity-nesting community by creating large durable cavities that provide breeding sites for large-bodied cavity-nesting ducks and raptors.

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APPENDIX. Cavity-nesting bird and mammal species present at sampling sites in interior British Columbia, 1995–2002.

Species	Code
Primary excavators	
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	RNSA
Hairy Woodpecker (*Picoides villosus*)	HAWO
American Three-toed Woodpecker (*Picoides dorsalis*)	TTWO
Black-backed Woodpecker (*Picoides arcticus*)	BBWO
Northern Flicker (*Colaptes auratus*)	NOFL
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO
Weak excavators	
Downy Woodpecker (*Picoides pubescens*)	DOWO
Black-capped Chickadee (*Poecile atricapillus*)	BCCH
Red-breasted Nuthatch (*Sitta canadensis*)	RBNU
Secondary cavity nesters	
Wood Duck (*Aix sponsa*)	WODU
Bufflehead (*Bucephala albeola*)	BUFF
Barrow's Goldeneye (*Bucephala islandica*)	BAGO
Hooded Merganser (*Lophodytes cucullatus*)	HOME
American Kestrel (*Falco sparverius*)	AMKE
Northern Saw-whet Owl (*Aegolius acadicus*)	NSWO
Northern Hawk Owl (*Surnia ulula*)	NHOW
Tree Swallow (*Tachycineta bicolor*)	TRES
Mountain Chickadee (*Poecile gambeli*)	MOCH
Mountain Bluebird (*Sialia currucoides*)	MOBL
European Starling (*Sturnus vulgaris*)	EUST
Northern flying squirrel (*Glaucomys sabrinus*)	GLSA
Bushy-tailed woodrat (*Neotoma cinerea*)	NECI
Red squirrel (*Tamiasciurus hudsonicus*)	TAHU
Chipmunk spp. (*Eutamias* spp.)	
Short-tailed weasel (*Mustela erminea*)	MUER
Deer mouse (*Peromyscus maniculatus*)	PEMA
Bark nesters	
Brown Creeper (*Certhia americana*)	BRCR