Characteristics and Dynamics of Cavity Nest Trees in Southern British Columbia[1]

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Abstract

We report on the characteristics, persistence, and temporal use patterns of nest trees of cavity-nesting wildlife in coniferous forests of southern British Columbia, Canada. Our goal is to identify the types of trees required to be retained during forestry operations if viable populations of cavity nesters are to be maintained in managed forests. Between 1994 and 1999, we recorded nesting species and tree characteristics during the year of first detection of active nest trees and in subsequent years, to document changes in wildlife use and tree condition. We located a total of 602 nests of 16 cavity-nesting species in 420 trees. Predominant tree species with active nests were Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). More than half of all nest trees were dead and/or partially broken when first detected. Three to 4.5 percent of nest trees were lost due to uprooting or total breakage each year. Partial breakage occurred at average annual rates of 1.1 to 6.2 percent each year. During the study period, 30 percent of nest trees were reused by breeding cavity nesters.

Introduction

Trees suitable for cavity excavation are an essential resource for wildlife species that require cavities in trees for breeding, roosting, and shelter from inclement weather and predators. The suitability of trees for cavity excavation is primarily determined by their size and the degree and pattern of decay present in the main stem or major branches of trees (Bull and others 1997). However, patterns of use may differ among cavity nester guilds and over time. Cavity nesters are typically grouped as strong excavators (i.e., woodpeckers) and weak excavators (i.e., nuthatches and chickadees)—both of which groups excavate their own cavities—and secondary cavity nesters (e.g., squirrels, bluebirds, swallows, and tree-nesting ducks and owls), which use cavities created by woodpeckers, broken branches, or wood decay processes (McClelland and others 1979, Newton 1994). Trees with cavities are often used repeatedly over time, either by the same breeding pair, by different pairs of the same species, or by multiple species either sequentially or simultaneously (Daily and others 1993, Loeb 1993, Sedgwick 1997). The dependence of secondary cavity nesters on the excavations of primary cavity nesters has been well established (Machmer and Steeger 1995).

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Numerous studies have examined attributes of trees preferred by various cavity nesters (Bate 1995, Bull and others 1997, Harestad and Keisker 1989, Raphael and White 1984, Sedgwick and Knopf 1990, Steeger and Hitchcock 1998). Because nest-site availability can be dramatically altered by forest-cutting regimes (Zarnowitz and Manuwal 1985), active nest trees with potential for reuse are among the most important wildlife habitat components that require retention in forestry operations. There is, however, general lack of information on the longevity and repeated use of nest trees.

In this paper, we report on cavity nesters and their choice of nest tree characteristics (i.e., tree species, condition, and size), rates of complete loss or partial breakage of nest trees, and reuse of nest trees by breeding cavity nesters in coniferous forests of southern British Columbia, Canada. Our primary objectives are to examine condition and use of cavity nest trees over time and provide management recommendations for nest-tree retention in operational forestry.

Study Area

We conducted surveys for breeding cavity nesters in the 9,000-hectare Deer Creek watershed of Arrow Forest District, in the Columbia River basin of southern British Columbia (49°30'N, 118°00'W). Elevation of the area surveyed ranges from 500 to 1,450 meters, and the area is generally southwest-facing. Most of the stands surveyed are managed stands of mature forest (85 to 95 years). Dominant conifer species are Douglas-fir *(Pseudotsuga menziesii),* lodgepole pine *(Pinus contorta),* and western larch *(Larix occidentalis),* with a minor component of localized western redcedar *(Thuja plicata),* western hemlock *(Tsuga heterophylla),* western white pine *(P. monticola),* and ponderosa pine *(P. ponderosa).* The minor hardwood component is dominated by trembling aspen *(Populus tremuloides)* and paper birch *(Betula papyrifera).* The most significant forest insects and pathogens include endemic populations of mountain pine beetle *(Dendroctonus ponderosae),* root disease *(Armillaria ostoyae),* and larch dwarf mistletoe *(Arceuthobium laricis).* Based on visible fungal fruiting bodies, common heart-rot fungi responsible for the wood decay that facilitates cavity excavation by primary cavity nesters include white spongy trunk rot *(Fomes fomentarius),* hardwood trunk rot *(Phellinus igniarius)* and aspen trunk rot *(Phellinus tremulae)* on broad-leafed tree species, and red ring rot *(Phellinus pini)* and brown crumbly rot *(Fomitopsis pinicola)* on conifers. Snag densities varied throughout the study area. Some managed stands contained hardly any snags (less than 1 snag per hectare), whereas other stands contained low to moderate densities (10 to 50 snags per hectare). Unmanaged stands with relatively high levels of *Armillaria* root disease contained high densities of snags (greater than 100 snags of 10 cm diameter at breast height or more per hectare; Steeger and Machmer 1995).

Methods

Nest Searching

We conducted nest searches in approximately 50 percent (4,500 hectare) of the Deer Creek watershed, primarily in areas where road access facilitated ground surveys. We searched for active nests of cavity nesters between May and early July 1996 to 1999 by inspecting trees for cavities, examining the ground for fresh wood chips, following adult birds, and listening for begging chicks. We considered a nest cavity to be active if a bird or mammal was observed incubating eggs or caring for young. Most trees were visited at least twice each breeding season to confirm occupation.

Nest Tree Assessments

For each confirmed active nest tree, we recorded tree species, tree diameter at breast height (dbh) measured with a dbh tape, tree height measured with a clinometer, tree condition (alive, dead, hard or soft snag), and location using a global positioning system device. We also noted presence of broken tops or stems, fungal decay (on the basis of visible conks), old excavated cavities, and identified the species of cavity nester using the tree.

We revisited nest trees at least twice during the survey period (no reassessments were conducted in 1995) to determine current tree condition (i.e., unchanged, uprooted, partially or completely broken). We also examined each tree for evidence of new nesting, visually and by tapping on trees. Most breeding cavity nesters were easily flushed from their cavities by this method, with the exception of red squirrels. Our sample, therefore, may underestimate cavity occupancy by red squirrels.

For data analysis on the choice of nest trees by cavity nesters, we took into account that a subset of nest trees contained more than one nest over the study period. To avoid potential pseudoreplication of individual cavity nesters, we removed additional nests of the same cavity-nesting species from the nest tree data set, if individual nest trees were occupied repeatedly by the same species. We performed statistical analyses with JMP statistical software[4] (Sall and Lehman 1996). With respect to the descriptions of nest trees, our study reports on use but not on availability of nest trees; hence, no inference about preference for certain trees can be made.

Results

Cavity Nesters and Their Nest Trees

From 1994 to 1999, we found seven woodpecker, four weak excavators, and five secondary cavity-nesting species *(table 1)* occupying a total of 602 active nests. The proportional distribution of woodpeckers, weak excavators, and secondary cavity nesters in our sample was 59, 26, and 15 percent, respectively. The sample was dominated by 207 red-naped sapsucker and 117 red-breasted nuthatch nests, which together comprised about 54 percent of the sample.

[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Table 1—*Tree species used by cavity nesters for breeding in the Deer Creek watershed, southern British Columbia, 1994-1999*[1].

Wildlife species	n[3]	Tree species[2]							
		Tr As	Pa Bi	We La	Do Fi	Lo Pi	Po Pi	WR Ce	WW Pi
Woodpeckers:	263	47	24	14	7	4	4	0.4	0
Red-naped sapsucker *Sphyrapicus nuchalis*	138	51	38	4	7	0	1	0	0
Hairy woodpecker *Picoides villosus*	46	52	20	28	0	0	0	0	0
Northern flicker *Colaptes auratus*	36	50	8	19	11	0	11	0	0
Three-toed woodpecker *Picoides tridactylus*	23	9	0	30	9	43	4	4	0
Pileated woodpecker *Dryocopus pileatus*	11	73	0	0	0	0	27	0	0
Black-backed woodpecker *Picoides arcticus*	6	0	0	66	33	0	0	0	0
Downy woodpecker *Picoides pubescens*	3	66	0	0	33	0	0	0	0
Weak excavators:	148	17	21	15	42	3	2	0.7	0
Red-breasted nuthatch *Sitta canadensis*	110	7	19	15	54	2	3	0	0
Blacked-capped chickadee *Poecile atricapillus*	15	33	53	0	13	0	0	0	0
Mountain chickadee *Poecile gambeli*	12	50	8	33	0	8	0	0	0
Chestnut-backed chickadee *Poecile rufescens*	11	55	9	9	9	9	0	9	0
Secondary cavity nesters:	84	17	25	36	4	12	2	2	2
Northern flying squirrel *Glaucomys sabrinus*	45	29	33	22	4	9	0	2	0
Red squirrel *Tamiasciurus hudsonicus*	19	0	32	47	5	11	0	5	0
Brown creeper *Certhia americanus*	18	0	0	56	0	22	11	0	11
All species combined	495	33	23	18	17	5	3	0.8	0.4

[1] Numbers are percent of each sample (n = number of nest trees).
[2] TrAs = trembling aspen, PaBi = paper birch, WeLa = western larch, DoFi = Douglas-fir, LoPi = lodgepole pine, PoPi = ponderosa pine, WRCe = western redcedar, WWPi = western white pine.
[3] American kestrel *(Falco sparverius)* and Common goldeneye *(Bucephala clangula)* had a sample size of 1 and were in a trembling aspen and western larch, respectively.

Nest Tree Species

A total of 420 nest trees (containing 602 nests) were occupied by cavity nesters over the six breeding seasons. Some trees contained more than one nest, concurrently or in different years, and of the same or a different cavity-nesting species. Discounting 107 potentially pseudoreplicated nests, a total of 495 nests of different species were observed in the 420 nest trees. Eight tree species were used for nesting *(table 1)* of which, in order of most frequent use, trembling aspen, paper birch, western larch, and Douglas-fir accounted for most (91 percent) nest trees. Use of the four most-commonly used tree species by cavity-nesting guilds was significantly different from expected frequencies (chi-square = 134; d.f. = 6; $p < 0.0001$; *table 1*). In addition, pair-wise comparisons between guilds indicated different use patterns of tree species ($p < 0.001$ for all three comparisons). However, some similarities existed: woodpeckers and the secondary cavity-nesting guild (especially squirrels that use woodpecker cavities) primarily nested in aspen, birch and larch, whereas weak excavators most often used Douglas-fir. Aspen was used more often for nesting than any other tree species by five of the seven woodpecker species. A total of 75 percent of the 16 cavity-nesting species used aspen at least once.

The three-toed woodpecker used mostly coniferous species, especially larch and lodgepole pine (30 and 43 percent, respectively). Douglas-fir was very important to one species in particular, the red-breasted nuthatch, accounting for 54 percent of its nests. All cavity-nesting species with a nest sample greater than two used more than one tree species for nesting. The pileated and black-backed woodpeckers appeared to be selective in our study area with respect to tree species, using only two species: aspen and ponderosa pine and larch and Douglas-fir, respectively. Four cavity-nesting species showed considerable flexibility with respect to the species of tree they chose to nest in: three-toed woodpecker, red-breasted nuthatch, chestnut-backed chickadee, and northern flying squirrel each used six different tree species.

Nest Tree Condition

With the exception of aspen, most nest trees of all species (particularly ponderosa pine and Douglas-fir) were dead at the time of first detection *(fig. 1)*. Dead nest trees were predominantly classified as hard snags, except for Douglas-fir, most of which were classified as soft snags *(fig. 1)*. A high proportion of Douglas-fir, ponderosa pine and birch were partially broken and a high proportion of birch had visible evidence of wood decay (i.e., conks) *(fig. 1)*.

More than half (55 percent) of 495 nest trees located in this study were dead when first recorded with an active nest *(table 2)*. Selection of dead trees for nesting differed among the three guilds (chi-square = 55.5; d.f. = 2; $p < 0.0001$). Woodpeckers used living trees more than dead trees, whereas weak excavators used primarily dead trees and did so more than did secondary cavity nesters (Fisher's exact 2-tailed test; d.f. = 1; $p = 0.06$). The trend for woodpeckers to use living trees for nesting, however, is largely a result of their extensive use of living aspen. Removing aspen from this analysis shows that the majority of woodpecker nests (63 percent of 139 nests) were also located in dead trees. The proportional use of dead trees by individual cavity nesters (with sample size greater than 5) ranged from 33 – 50 percent in woodpeckers, 18 – 89 percent in weak excavators, and 51 – 94 percent in secondary cavity nesters. Almost all brown creeper nests found were in dead trees and constructed behind loose bark rather than in cavities in the stem or major branches of trees.

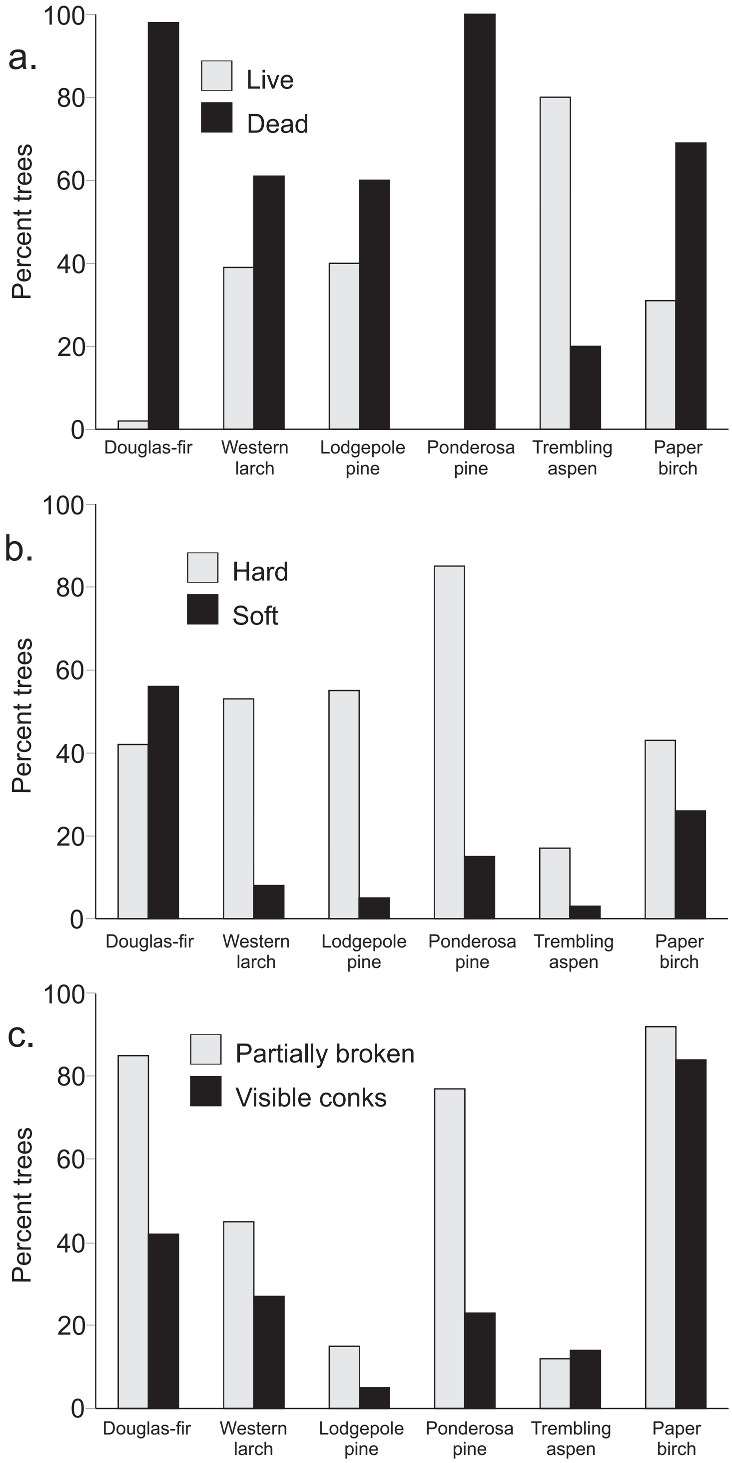

Figure 1—Proportion of nest trees that were (a) either living or dead, (b) dead with hard or soft stemwood, and (c) partially broken (> 2 meters standing) and/or showing visible sign of fungal decay (conks) in the Deer Creek watershed, southern British Columbia.

Table 2—*Proportion of nest trees that were dead when used by cavity nesters in the Deer Creek watershed, southern British Columbia, 1994-1999.*

Wildlife species	n[1]	Percent dead nest trees
Woodpeckers:	263	40
Red-naped sapsucker	138	41
Hairy woodpecker	46	33
Northern flicker	36	36
Three-toed woodpecker	23	48
Pileated woodpecker	11	36
Black-backed woodpecker	6	50
Downy woodpecker	3	67
Weak excavators:	148	76
Red-breasted nuthatch	110	89
Blacked-capped chickadee	15	60
Mountain chickadee	12	33
Chestnut-backed chickadee	11	18
Secondary cavity nesters:	84	4
Northern flying squirrel	45	51
Red squirrel	19	68
Brown creeper	18	94
All species combined	495	55

[1]American kestrel and Common goldeneye had a sample size of 1 and were in a live and dead tree, respectively.

Nest Tree Size

Comparison of the six tree species that contained more than one percent of active *(table 1)* showed that the interquartile range of diameter values increased with increase in median, with ponderosa and lodgepole pine showing the widest and narrowest range, respectively *(fig. 2)*. Mean diameters of nest trees differed significantly among the conifers ($F_{3,185}$ = 14.1; $p < 0.0001$); however, post-hoc comparison of means between the two most commonly-used conifer species, Douglas-fir and western larch, indicated no significant difference (Tukey Kramer test $\alpha = 0.05$). The two species of broad-leafed nest trees, trembling aspen and paper birch, also differed significantly in mean diameter ($t_{1,223}$ = 4.6; p $p < 0.0001$), and were, on average, smaller in diameter than the coniferous nest trees ($t_{1,412}$ = 6.2; $p < 0.0001$). Douglas-fir nest trees showed the second largest mean diameter, despite being used primarily by small-sized, weak excavators *(table 1*). For all tree species, 90 percent of all nest trees were larger than 18.5 cm in diameter.

Comparison of the three cavity nester guilds showed similar patterns of the range of diameter values around the median *(fig. 2)*, especially between woodpeckers and secondary cavity nesters. Mean diameters of nest trees did not differ significantly ($F_{2,418}$ = 1.08; $p = 0.34$) among the three guilds of cavity nester. Ninety percent of nest trees used by woodpeckers and secondary cavity nesters were larger than 23.1 cm in diameter, while 90 percent of nest trees used by weak excavators were larger than 16.4 cm in diameter.

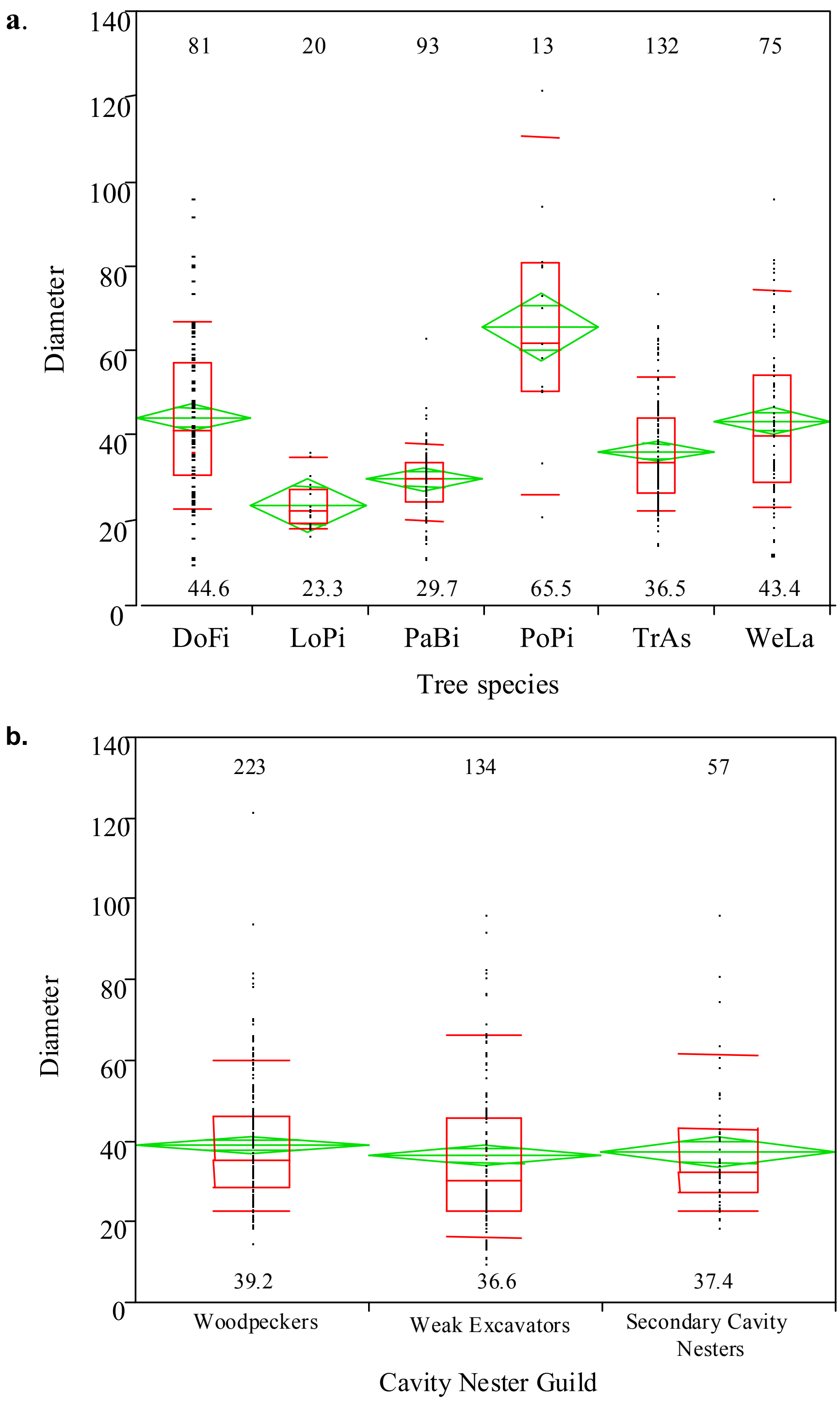

Figure 2—Central tendencies and associated variations in diameter (cm) values of nest trees by tree species (a) and cavity nester guild (b), Deer Creek watershed, southern British Columbia. Shown are distribution of all points, quantile box plots with medians, interquartile ranges (boxes) and 10 percent and 90 percent quantile lines, and means diamonds with means (center lines) and 95 percent confidence intervals (top and bottom of the diamonds). Sample sizes and mean values are given at the top and bottom of the panels, respectively.

Nest Tree Dynamics

Changes in Nest Tree Conditions

We considered all trees with active nests located within one season as a "nest-tree cohort" *(table 3)*. Over time, trees within a cohort either changed condition (e.g., they partially broke) or they were completely lost due to total breakage, uprooting, or forestry operations (i.e., tree cutting or road building). Over the study period, the average annual rate of nest tree loss due to natural causes (range: 3.0 to 4.5 percent/year, *table 3*) was fairly constant for each cohort, although there were differences in rates between the causes of tree loss. The annual proportion of nest tree loss due to natural causes for individual years (n = 15 for the five cohorts) ranged from 1.5 to 6.1 percent (data not shown). Average annual rates of partial tree breakage were generally similar to those for complete losses. We also report annual rates of nest tree loss due to forestry operations for comparative purposes, although these values are based on forest management decisions and vary accordingly. For the oldest nest-tree cohort (1994), we observed a total reduction in available nest trees of 48.5 percent over the 5-year period *(fig. 3)*.

Table 3—*Changes in nest-tree cohorts found annually from 1994-98; numbers are average (except for the 1998 cohort) annual rates of change (in percentages) of the original samples.*

	Nest-tree cohorts (initial number of trees)				
	1994 (66)	**1995 (99)**	**1996 (70)**	**1997 (64)**	**1998 (89)**
Tree loss due to natural causes: [1]	3.0	3.0	3.8	3.1	4.5
Trees partially broken (> 2 meters standing)	5.1	6.5	2.8	3.1	1.1
Tree loss directly due to forestry operations	6.7	3.3	0.9	1.6	2.3

[1]Causes included total breakage (< 2 m standing) or uprooting. Note that uprooting of some trees may have been indirectly caused by forestry operation via windthrow along the margins of cutblocks or roads.

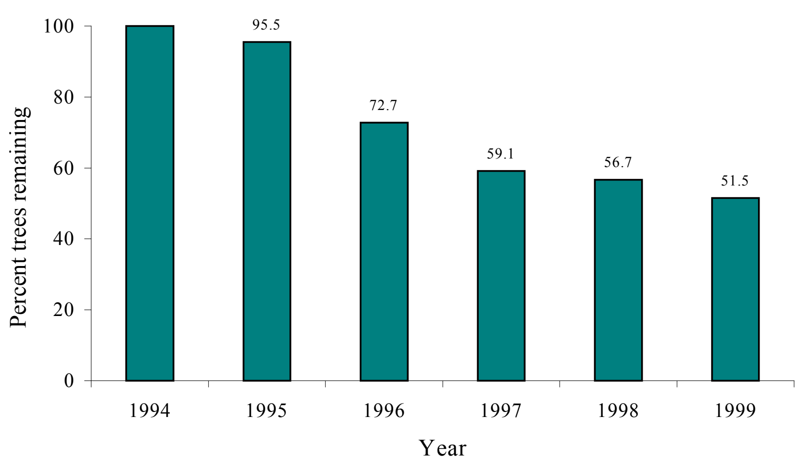

Figure 3—Reduction of the 1994 nest tree cohort (initial n = 66 nests) over 5 years in the Deer Creek watershed, southern British Columbia. Partially broken trees (> 2 meters standing) are included.

Reuse of Nest Trees

All tree species showed multiple excavated (nest or roost) cavities in individual trees, but there was a wide range of variation in the average and maximum number of cavities among species *(table 4)*.

Table 4—*Number of excavated cavities in individual trees, by tree species, in the Deer Creek watershed, southern British Columbia, 1994-1999.*

Species	n	Mean # of cavities (s.e., range)
Trembling aspen	132	3.6 (0.3, 1-14)
Ponderosa pine	13	3.4 (1.0, 1-11)
Paper birch	93	2.9 (0.3, 1-14)
Western larch	75	2.5 (0.3, 1-14)
Douglas-fir	81	2.0 (0.1, 1-7)
Lodgepole pine	20	1.2 (0.2, 1-4)

Reuse of nest trees involving new cavity excavation is generally higher in broad-leafed trees compared to conifers, primarily due to the woodpeckers' (especially red-naped sapsucker) frequent use of living aspen *(table 1, fig. 1)*. Among conifers, ponderosa pine and larch showed relatively high mean, maximum and variation in number of cavities. Lodgepole pine had the lowest mean, maximum and variation in number of cavities *(table 4)*; we only detected three-toed woodpeckers and the occasional weak excavator constructing nest cavities in lodgepole pine *(table 1)*. Overall, we detected multiple excavated cavities in 55.5 percent of all nest trees ($n = 420$), with larger trees containing more cavities than smaller trees ($r = 0.13$, $P < 0.01$). The proportion of trees with different numbers of multiple cavities was:

Number of cavities	Percent of nest trees
2	18.6
3	11.2
4	7.9
5	4.8
6	5.7
7-14	7.4

During the study period, 30 percent of all available nest trees ($n = 385$) were reused, by the same and/or one or more different species in at least one subsequent year. Reuse by the same, one or two different species occurred in 19, 14, and 2 percent of nest trees, respectively. We observed two simultaneously active cavity nests in 4 percent of all nest trees ($n = 420$), always by two different cavity-nesting species. The frequency of reuse of nest trees (maximum = five times) and the proportion of trees in each category was: once = 21 percent, twice = 5 percent, three times = 2 percent, four times = 0.8 percent and five times = 0.3 percent.

Discussion

Cavity nesters detected within our study area used a total of eight tree species for breeding sites, with variation in the pattern of use among the different cavity-nesting species and guilds. Based on the tree species used and the condition of nest trees, woodpeckers primarily used living trees (e.g., aspen) and hard snags (e.g., larch and lodgepole pine) for nesting. The pileated and black-backed woodpeckers were found in only two tree species which is consistent with the results of an extensive woodpecker study by Bull (1980). Our sample sizes for these species are low, however, and both species have been reported breeding in tree species different from the species reported in this study (Bull 1980, Raphael and White 1984). We found weak excavators nesting mostly in dead trees with advanced decay (e.g., Douglas-fir killed by *Armillaria* root disease and infected by *Phellinus pini*) and in partially broken trees. Red-breasted nuthatches, for example, most often nested near the break of broken-top trees (Steeger and Hitchock 1998). Eighty-five percent of 110 nuthatch nest trees located in the present study were partially broken. While we recorded presence of visible conks on nest trees, many living trees did not show any sign of fungal wood decay. However, because they were excavated by primary cavity nesters, they likely contained some wood decay at the level of the nest cavities (Conner and Locke 1982, Parks and others 1996). Most nest trees in our study were dead.

Ponderosa and lodgepole pine nest trees showed the highest (65.5 cm) and lowest (23.3 cm) mean diameter, respectively. We do not have information on the proportions of different tree species and their diameter distributions in the study area and therefore cannot address preference for certain species and diameters by breeding cavity nesters. However, preference for large-diameter snags has been well documented for a variety of cavity nesters (see references in Bull and others 1997). In our study, mean diameter of all nest trees was 38.1 cm. Mean diameter of nest trees of woodpeckers, weak excavators, and secondary cavity nesters was 39.2 cm, 36.7 cm, and 37.1 cm, respectively. These mean diameter (dbh) values are notably lower than those reported for cavity nest trees by, for example, Mannan and others (1980; greater 60 cm in western Oregon), Raphael and White (1984; 62.3 cm in northern California), and Lundquist and Mariani (1991; 75.8 cm in southern Washington) but are similar to those reported by Harestad and Keisker (1989; 32.3 cm in southcentral British Columbia). This difference in mean nest tree diameter between these United States and British Columbia studies may be related to the tree species and their diameter distribution available for cavity nesting in the respective study areas. However, regardless of the reason for this difference, our study shows that trees less than 40 cm in diameter are frequently used for cavity nesting, but we do not know the reproductive success of the breeding pairs we observed. A valuable contribution by further studies on cavity nest trees would be to examine reproductive success of pairs breeding in trees within a range of different characteristics.

Average annual nest tree losses due to natural breakage or uprooting (i.e., not directly caused by tree cutting) ranged from 3.0 to 4.5 percent. These values are higher than the average annual 1.7 and 1.1 percent reported for attrition of pileated woodpecker nest trees by Bull (1987) and Bonar (2000), respectively. Our sample included nest trees of 16 cavity-nesting species, some of which are weak excavators that generally breed in dead and more decayed trees with presumably higher fall rates than those reported by Bull (1987) and Bonar (2000). The fall rates in our study are lower than those reported by McCelland (1977) who observed for seven cavity nesters a loss of 9 out of 83 nest trees over 2 years (or 5.4 percent annually), but at least two of his nine trees were cut. The average annual rates of nest tree losses documented in our study are based on annual cohorts of all nest trees sampled. Therefore, the rates primarily represent nest tree loss of the most common nest tree species (i.e., aspen, birch, Douglas-fir, and larch) together. Rates of individual species may differ and will be evaluated when sample sizes are sufficient.

Most nest trees (55.5 percent) in this study showed evidence of multiple cavity excavation. The number of multiple cavities in some trees may be underestimated as trees that were partially broken when first detected may have had other cavities in the part of the trunk that had broken off. Also, because more than half of all nest trees already contained two or more excavated cavities when first detected, our values for reuse of nest trees are potentially underestimates and some cavities may have gone undetected. Multiple nest cavities in trees have previously been documented by Sedgwick and Knopf (1986), who found 38.5 percent of all cavity trees had multiple excavations and that, consistent with our results, larger trees had more cavities than smaller trees. The observed multiple use of large-sized trees by cavity nesters, either sequentially over several years or simultaneously, indicates the high habitat and conservation value of such trees.

Management Implications

The low-elevation coniferous forests of the southern interior of British Columbia are characterized by a high diversity of tree species (Meidinger and Pojar 1991) that supports a variety of primary and secondary cavity nesters. Seven sympatric woodpecker species occur in our study area, which is near the maximum number reported for North America (Short and Horne 1990). Because woodpeckers and other cavity nesters play important ecological roles in forest ecosystems (e.g., regulation of insect populations, [Machmer and Steeger 1995], keystone cavity excavators in nest webs [Martin and Eadie 1999]) and are potentially negatively affected by intensive forestry, preservation of their nest trees has become part of forest management in British Columbia.

Although some tree species such as aspen and larch are used by a variety of cavity nesters, other tree species are used by only a few individual cavity nesters (e.g., use of lodgepole pine by three-toed woodpeckers). Retention of nest trees during forestry and other land-use operations, therefore, may be most beneficial to the diversity of cavity nesters if sets of tree species are retained that are representative of the pre-harvest stand composition. Of particular importance for any retention strategy are broad-leafed trees with evidence of nest cavities, especially in stands in which these species constitute a minor component of the tree species composition. Large-diameter ponderosa pine snags are important nest trees for woodpeckers potentially over long periods of time, as indicated by the high number of nest cavities they contain in our study area; they should be retained wherever possible. In stands with high levels of bark beetle populations, selective harvesting of infested or susceptible pine should include some pine retention to provide current and future nesting as well as foraging opportunities, especially in three-toed woodpecker home ranges.

For cavity nesters in general, dead and partially broken coniferous and broad-leafed trees and trees with fungal wood decay are essential habitat components. Under endemic levels of natural disturbance agents (insects and diseases) and in the absence of catastrophic winds and fires, the annual rate of nest tree loss due to natural causes is less than 5 percent in our study area and may be in balance with new trees becoming suitable for cavity nesting. However, forestry operations such as road building and logging along with unregulated firewood cutting can lead to dramatic reductions in habitat for cavity nesters over extensive areas of the landscape. Because primary cavity nesters are territorial during the breeding season (i.e., they exclude conspecifics from a given area), establishment of zones where intensive forestry is practiced without retention of dead and diseased trees will lead to declines in cavity nester populations, as these zones will not be able to contain more breeding pairs as set by the species' territory size requirements. Cavity nester populations fluctuate naturally in any given area according to the often ephemeral availability of essential resources such as nest sites and feeding opportunities (Baldwin 1968, Otvos 1979). However, elimination of dead and diseased trees that provide habitat for cavity nesters is a systematic and, to some extent, inevitable process in industrial forestry that most probably effects the natural dynamics of populations. If intensive forestry zones are too wide-spread, species of cavity nesters may become endangered or locally extirpated as, for example, in the managed taiga forests of Sweden that are suffering severe losses of broad-leafed and dead trees (Angelstam 1990, Angelstam and Mikusinski 1994). In British Columbia, the Wildlife/Danger Tree Assessor's Course and the recently revised occupational health and safety regulations of the Workers' Compensation Board now allow for retention of dead trees in all forestry operations, provided they do not pose a hazard to forest workers (Manning and others 2002). Successful implementation of these new initiatives will be an important step in conserving the habitat of cavity nesters in British Columbia.

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