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NEST TREE SELECTION BY PRIMARY CAVITY-NESTING BIRDS IN SOUTH-CENTRAL BRITISH COLUMBIA

by

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ABSTRACT

I examined use and selection of nest trees by 6 species of primary cavity-nesting birds in the Interior Douglas-fir Biogeoclimatic Zone (IDF) near Kamloops, British Columbia. Analyses were based on 243 active nests located during 1984 and 1985.

Presence of heartwood decay was the most important tree characteristic influencing selection of nest trees; all bird species strongly preferred trees bearing fruiting bodies of heartrot fungi. Most nests occurred in trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and hybrid spruce (*Picea engelmannii* x *glauca*) were not used for nesting, probably because their pattern of decay was unfavourable for cavity-nesting. However, dead conifers appeared to be important foraging substrates. In trembling aspen, infection with heartwood decay occurred in live trees, leaving a sound sapwood shell protecting nest holes excavated in the softened heartwood. Such trees were preferred by the stronger excavators, Yellow-bellied Sapsucker (*Sphyrapicus varius*), Pileated Woodpecker (*Dryocopus pileatus*), and Hairy Woodpecker (*Picoides villosus*) which were able to penetrate the hard sapwood. Weaker excavators, Red-breasted Nuthatch (*Sitta canadensis*), Northern Flicker (*Colaptes auratus*), and Downy Woodpecker (*Picoides pubescens*), preferred dead trees or dead tops of live trees for nesting. Yellow-bellied Sapsucker preferred to nest in trees larger than 30 cm dbh, and Pileated Woodpecker preferred trees larger than 40 cm dbh. No significant preference for nest tree diameter was detected for the other species. Results were very similar when analyses were based on old, unoccupied cavities instead of active nests.

Stands containing deciduous trees were strongly preferred to coniferous forest for nesting. Structural variation of the vegetation within the deciduous or mixed stands had very little influence on nest tree selection.

Trees with attributes preferred for nesting occur as part of the deciduous, maturing and overmature seral vegetation, which is replaced by coniferous climax forest as succession

proceeds. Uneven-aged forest management and fire suppression create adverse conditions for establishment of deciduous stands. To ensure continuous availability of nesting habitat for primary cavity-nesters over time, a mosaic of successional stages should be maintained by periodically creating openings in sites suitable for regeneration of deciduous trees.

Tree species differ in their decay characteristics, their ecology, and in the role they play in forest management. Nest tree preferences and management guidelines outlined in my study may therefore not be relevant to areas, where species other than trembling aspen and paper birch are important for nesting.

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CHAPTER 1

INTRODUCTION

Cavity-nesting birds require tree cavities in which to raise their young. Primary cavity-nesting birds usually excavate their nest holes themselves, whereas secondary cavity-nesters generally nest in existing tree cavities. To build their nest and roost cavities, primary cavity-nesting birds require trees with decay. This group of birds is therefore adversely affected by habitat alterations that reduce the availability of dead or decaying trees, such as intensive forest management or fuelwood cutting. Awareness of the importance of so-called decadent trees to cavity-nesters and other species has increased in recent years. However, efforts to prevent further depletion of these "wildlife trees" are impeded by a number of obstacles, related mainly to timber production goals, safety considerations, and knowledge gaps. These problems were investigated in detail by Miller (1985) in relation to wildlife tree management in British Columbia.

Specific knowledge of the nesting habitat needs of primary cavity-nesting birds is an important prerequisite to maintaining these species in managed forests. The purpose of my study was to collect this information for a part of the Interior Douglas-fir Biogeoclimatic Zone, IDF (Krajina 1965), in British Columbia. Much is known about the biology and habitat requirements of primary cavity-nesting birds (see Thomas 1979, Fischer and McClelland 1983 for bibliographies) and effects of forest management on primary cavity-nesters have been examined in a number of studies (Shugart and James 1973, Conner and Crawford 1974, Conner et al. 1975, Conner and Adkisson 1975, 1976, 1977, Franzreb 1977, Evans 1978, Franzreb and Ohmart 1978, Conner et al. 1979, Scott 1979, Szaro and Balda 1979, Dickson et al. 1983, Dingledine and Haufler 1983, Marcot 1983, Scott and Gottfried 1983, Raphael and White 1984, Madsen 1985, Wood et al. 1985, Zarnowitz and Manuwal 1985). However, almost all this information is based on studies conducted in various regions of the United States and results and management suggestions may not be applicable to the IDF.

The objectives of my study were:

1. to examine nest tree use and identify attributes that characterize trees preferred for nesting by primary cavity-nesting birds in part of the IDF,
2. to compare results with published findings of similar studies conducted in other vegetation types and geographical areas,
3. to evaluate effects of forestry practices and develop management guidelines aimed at integrating forestry and nesting habitat needs of primary cavity-nesting birds.

CHAPTER II

STUDY AREA

Most fieldwork was conducted within and just south of three adjacent cutting permits (#526, 516, and 'H', held by Balco Industries Ltd.), which are located in Timber Sale Licences A18686 and A07212 in the Kamloops Forest Region. This area, known locally as the Orchard Lake Area, extends along a portion of the Sullivan Range which runs along the east side of the North Thompson River (Fig. 1). The Orchard Lake Area is approximately 38.5 km north and 9.0 km east of Kamloops, British Columbia, and centers at 51°01'20" N and 120°11'15" W. It comprises approximately 2041 ha and lies between elevations 610 m (crest of the North Thompson Valley) and 910 m (transition to a different forest type).

The Orchard Lake Area lies within the IDFa Biogeoclimatic Subzone (Very Dry Submontane Interior Douglas-fir). Its overall topography is formed by a series of north-south ridges. Many of the draws contain small ponds and lakes. Most of the area is covered by coniferous forest, which consists almost entirely of Douglas-fir. Birch-leaved spirea (*Spirea betulifolia*) and waxberry (*Symphoricarpos albus*) are the main species forming the generally sparse understory vegetation. Patches of natural grassland with scattered Douglas-fir extend along the ridgetops. Stands of deciduous trees, mainly trembling aspen and paper birch, with varying proportions of Douglas-fir and hybrid spruce, grow in moister or disturbed sites. Black cottonwood (*Populus trichocarpa*) and thin-leaved mountain alder (*Alnus incana*) occur in sites subject to flooding. Dominant shrub and herb species in these deciduous or mixed stands vary among sites. Common species are Douglas maple (*Acer glabrum* var. *douglasii*), saskatoon (*Amelanchier alnifolia*), heart-leaved arnica (*Arnica cordifolia*), northern twinflower (*Linnea borealis*), prickly rose (*Rosa acicularis*), and waxberry. Roads, landings, and other disturbed sites are usually seeded for cattle grazing and are dominated by cultivated grasses and associated weed species. For a detailed description of ecosystem associations within the IDFa, including information on climate, geology, and soils, see Mitchell and Green (1981).

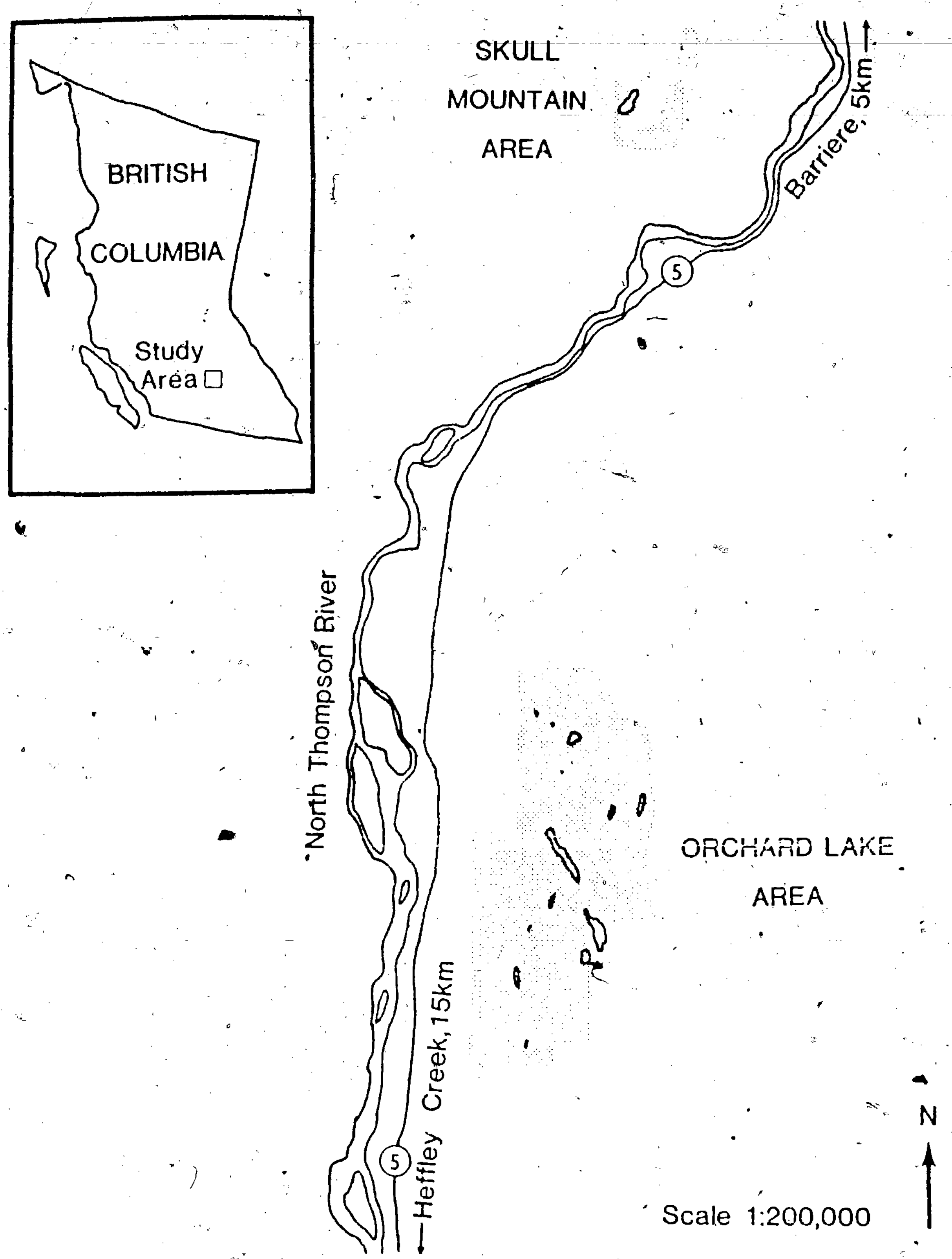

Fig. 1. Location of study area and its two parts, the Orchard Lake and Skull Mountain Areas.

The area was selectively logged during the 1930's when the largest conifers were harvested. Since 1975, parts of the area have been logged each year. For the past few years the cutting prescriptions for the area have been modified with the aim of maintaining all age classes of trees within the forest. Previously, selective logging usually consisted of cutting all trees that exceeded diameter limits specified in logging plans. Under current prescriptions, snags are usually left standing to serve as "wildlife trees" unless they pose a safety hazard.

Additional fieldwork was conducted in and near the Skull Mountain Area, a parcel of land acquired by the Ministry of Environment, mainly to preserve its value as critical winter range for Mule Deer (*Odocoileus hemionus*). This part of the study area lies on the south-eastern slope of a ridge that runs along the west side of the North Thompson River, and is also part of the IDFa Biogeoclimatic Subzone (Fig. 1). Fieldwork in the Skull Mountain Area was confined to the vicinity of Corral Lake, and an area around a series of ponds approximately 4 km north-east from the lake along the access road. This portion of the study area comprised about 28 ha, with elevations ranging from 660 to 700 m. Corral Lake is located at 51° 07'25" N and 120° 10'25" W, 50 km north and 10 km east of Kamloops. Vegetation around the lake consists of open stands of paper birch and trembling aspen with some scattered Douglas-fir and ponderosa pine (*Pinus ponderosa*). There has been extensive clearing for cattle pasture, and grazing has since had an influence on the vegetation. The series of ponds are surrounded by open to dense stands of mixed deciduous/coniferous forest, similar to those in the Orchard Lake Area.

CHAPTER III

METHODS

Nest Search

I searched the study area for active nests of primary cavity-nesting birds during the breeding seasons of 1984 and 1985. In both years, most nests were found between mid-May and the end of June. During the initial phase of the nest search, between 18 and 31 May 1984, I searched about 250 ha of coniferous and 14 ha of deciduous or mixed forest. During this period and earlier reconnaissance walks throughout the study area (2-16 May), I observed that nesting activities of all species were restricted to stands containing deciduous trees. I therefore concentrated most of my nest search on stands of deciduous or mixed forest, which comprised a total of 104 ha, approximately 5% of the whole study area. The locations of these stands were mapped from aerial photographs with ground verification. Dead conifers, which were found to be important nest sites in many other studies, occurred scattered throughout my study area. The areal restriction of the nest search may thus have led to an underrepresentation of dead conifers among the trees examined for nesting use. To intensify the nest search with respect to snags, I examined a random sample of 105 dead conifers for evidence of nesting use. Random samples were chosen by laying out a uniform grid on a large scale map of the study area, and selecting coordinates using a table of random numbers.

Primary cavity-nesting birds usually excavate fresh nest cavities every spring. Nests were therefore located mainly by inspecting the ground around every tree for the presence of fresh woodchips and by examining the tree trunks for cavities. When woodchips were discovered and a fresh cavity entrance was located, the tree was struck with a baseball bat to flush birds from inside the cavity. This allowed identification of the bird species during the incubation period. The presence of a bird in the cavity was assumed to indicate an active nest. In cases where no flushing occurred – Pileated Woodpecker could never be flushed and Red-breasted Nuthatch were often reluctant to leave the cavity – the nest was confirmed by observing the cavity until a bird approached it and either entered or offered food to the bird inside. Later in the breeding season when young could be heard calling from within the cavities, their vocalizations confirmed the presence of an active nest and the bird species was identified by waiting for an adult to return to feed or brood the nestlings.

For practically all cases in which fresh woodchips were found and the cavity appeared to have been completed, I was able to confirm it as an active nest. Aborted cavity attempts could usually be identified by the scarcity of woodchips and the funnel shaped narrowing of the cavity entrance. The woodchips also revealed, by their position in relation to last year's leaf litter, whether the cavity had been excavated during the current or the previous season. The method of nest search described above was less reliable when few woodchips were produced, which occurred when old cavities were used for nesting as was sometimes observed for Red-breasted Nuthatch and Northern Flicker. Red-breasted Nuthatch added to the problem by sometimes carrying off the woodchips during nest excavation. Active nests with few woodchips were detected mainly by striking all trees in which cavities could be seen. Since cavities were more difficult to detect in dense stands and tall trees and birds were more easily flushed from short, decayed trees than from tall, sound ones, this method may have introduced a sampling bias. However, this problem may have been alleviated for Northern Flicker, because they always flushed very readily, often leaving the cavity before the nest tree was even struck. Identification of active nests of Red-breasted Nuthatch was facilitated by their habit of smearing the cavity entrance with resin and by their often noisy behaviour around their nest.

Nest Tree Description

Each nest tree was numbered and marked with flagging tape. The following information was recorded for each tree:

1. location (determined by taking compass bearings and by pacing distances in relation to landmarks identifiable on the map)
2. tree species
3. tree diameter (dbh, at 1.3 m above the ground)
4. tree height (using a clinometer, measured to top of crown or top of broken trunk)
5. tree condition:
   a. live with live top, live with dead top, or dead
   b. for dead trees or dead tops: condition of sapwood, condition of heartwood (if accessible), percent of bark remaining and its appearance, presence of dead foliage, twigs, and branches
6. presence of heartwood decay indicators: fungal fruiting bodies (conks), scars with exposed wood, broken tops
7. information pertaining to the active nest cavity:
   a. occupying bird species
   b. cavity type: freshly excavated, old, or natural
   c. for old cavities: suspected original excavator species
   d. height of cavity entrance above the ground (using a clinometer)
   e. condition of wood containing nest cavity: live or dead
   f. compass orientation of cavity entrance
   g. orientation of cavity entrance in relation to nearest tree
8. presence of feeding signs:
   a. sap drilling, small, medium, large holes, bark scaling, feeding observations
   b. bird species (if obvious)
9. presence of old, unoccupied cavities:
   a. number
   b. suspected excavator species
10. presence of unfinished cavities:
   a. number
   b. suspected excavator species

The location of each nest tree was plotted on a large scale map (1:10,000) of the study area. Most of the nests found were located in live trees so that decay classifications designed for snags, such as those of Thomas (1979) and Cline et al. (1980) were of limited use. Trees were examined for presence of the decay indicators shown in the above list, to obtain some indication of the condition of the heartwood without having to cut them down. Extent of decay was not assessed. An original plan to age every nest tree was abandoned because the prevalence of decay made it impossible to obtain a usable core.

Description of Available Trees

To obtain a measure of the species, sizes, and condition of trees available to the birds for nest tree selection, 181 circular random sample plots of 8 m radius (0.02 ha) were laid out in the deciduous or mixed stands. All trees within these plots that exceeded 15 cm in diameter and 1 m in height were described according to the same parameters listed above for nest trees. A total of 933 sample trees were assessed. None of the conifers that occurred interspersed with the deciduous trees contained nests. Only deciduous trees were therefore included in the sample representing available trees to avoid biasing the sample with characteristics of tree species that were not used for nesting.

Vegetation Description

In addition to examining tree characteristics, I described the immediate vicinity (8 m radius) of each nest tree and of the centre tree in each of the random plots. Vegetation characteristics noted were:

1. tree cover (%)
2. shrub cover (%)
3. herb cover (%)
4. distance to nearest tree
5. species of nearest tree
6. total basal area of all trees
7. total basal area of all trees $\geq$10 m in height
8. average canopy height of trees $\geq$10 m in height
9. maximum canopy height
10. number of live trees by height class (m) (1=1–4.9, 2=5–9.9, 3=10–14.9, 4=15–19.9, 5=20–24.9, 6$\geq$25)
11. total number of live trees
12. number of dead trees by height class
13. total number of dead trees
14. total number of trees
15. live trees in height classes 4–6 / live trees in height classes 1–3
16. all trees in height classes 4–6 / all trees in height classes 1–3
17. dead trees / live trees
18. trembling aspen / paper birch
19. deciduous / coniferous trees
20. Douglas-fir / spruce
21. other deciduous trees / trembling aspen and paper birch

Statistical Analyses

Characteristics of trees used for nesting were compared with a random sample of trees to determine whether particular types of trees were preferred for nesting. Differences between use and availability were tested for significance with Chi-square tests, to which Yates' continuity correction was applied in the case of 2x2 contingency tables. Calculations of selection indices and simultaneous confidence intervals, followed statistical techniques outlined by Strauss (1979), Marcum and Loftsgaarden (1980), and Byers and Steinhorst (1984). The level of significance accepted throughout this study is 95% ($P \leq 0.05$). The sample representing available trees was weighted, to equalize proportions of sample trees described in the Orchard Lake Area and Skull Mountain Area and proportions of nests found in the two areas.

A principal components analysis was conducted on the set of intercorrelated variables describing each nest tree, to summarize most information in the data within a small number of linear combinations of the original variables. Principal components scores obtained for each bird species were examined to reveal interspecific similarities and differences in nest tree characteristics. The relative value of the various tree variables as indicators of a tree's suitability as a nest site was assessed by means of a stepwise logistic regression.

Data were analysed using the SPSSx (SPSS Inc. 1983) and the BMDP statistical computer packages (BMDP Statistical Software 1981). Further explanation of statistical techniques is provided in conjunction with the results.

CHAPTER IV

RESULTS

Nest Sample

I found 243 active nests occupied by 6 species of primary cavity-nesting birds (Table 1). The nest sample was dominated by 159 nests of Yellow-bellied Sapsucker. Of the 20 Pileated Woodpecker cavities, only 8 were confirmed active nests. The rest were unconfirmed nests or roost cavities. Except for one confirmed roost, all of the Pileated Woodpecker cavities had been recently excavated, as indicated by fresh woodchips on the ground, and appeared to be completed. Although the occupying birds were not observed for all of these cavities, they were treated as confirmed Pileated Woodpecker cavities, since no other species in the area excavates holes of this size and shape. Seven Red-breasted Nuthatch nests and 3 Northern Flicker nests were in old cavities apparently excavated by other species. The suspected original excavator species were Yellow-bellied Sapsucker in the case of Red-breasted Nuthatch, and Pileated Woodpecker in the case of Northern Flicker. Red-breasted Nuthatch and Northern Flicker were classified as primary cavity-nesting birds since they had excavated most of their nest holes themselves. Five trees were used for nesting by 2 species of primary cavity-nesting birds during the same season (Red-breasted Nuthatch with Yellow-bellied Sapsucker or Hairy Woodpecker, Northern Flicker with Yellow-bellied Sapsucker, Pileated Woodpecker, or Hairy Woodpecker). Each of these trees were counted twice, once for each occupying species, since the tree had been selected by both. None of the Red-breasted Nuthatch and Northern Flicker nests in these 5 trees had been freshly excavated.

Toward the end of the breeding season, when young of some species had left the nest, a number of cavities of species other than Pileated Woodpecker were found that had been excavated earlier in the year and may have served as nests but were now abandoned. Although the bird species could not be confirmed, 10 of these cavities were included in the

Table 1. Numbers of active nests found for species of primary cavity-nesting birds breeding in the study area and tree species used for nesting.

Bird species	Number of nests found			
	Total	Trembling aspen	Paper birch	Thin-leaved mountain alder
Yellow-bellied Sapsucker	159	146	13	-
Pileated Woodpecker	20[1]	20	-	-
Hairy Woodpecker	8	8	-	-
Red-breasted Nuthatch	24	14	9	1
Northern Flicker	17	14	3	-
Downy Woodpecker	5	3	1	1
Species unconfirmed	10	8	2	-
Total	243	213	28	2

[1]includes 8 confirmed active nests and 12 roosts or unconfirmed nests

nest sample, because they showed strong evidence of use as nest cavities by primary cavity-nesting birds, such as pieces of white eggshell on the ground. The size and shape of these unconfirmed nests suggested that most of them were Hairy Woodpecker cavities. In both years, young of this species were the first primary cavity-nesting birds to fledge. Unconfirmed cavities were included only in analyses for which all bird species were pooled.

I found the following species of secondary cavity-nesters breeding in the study area: American Kestrel (*Falco sparverius*), Tree Swallow (*Tachycineta bicolor*), Black-capped Chickadee (*Parus atricapillus*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), Red Squirrel (*Tamiasciurus hudsonicus*), and Northern Flying Squirrel (*Glaucomys sabrinus*).

Nest Tree Characteristics

None of the conifers in the study area (mainly Douglas-fir and hybrid spruce) contained nests of primary cavity-nesting birds. Analyses of nest tree selection in this study are therefore based only on deciduous trees.

Tree species

Only 3 tree species were used for nesting by primary cavity-nesting birds (Table 1). Most nests occurred in trembling aspen. Paper birch was used much less frequently, and only 2 nests were found in thin-leaved mountain alder. The greater use of trembling aspen was evident for each bird species. Pileated Woodpecker and Hairy Woodpecker nested exclusively in trembling aspen.

This pattern of use, however, may simply be a reflection of the differential availability of these tree species in the forest. I therefore took a random sample of 933 deciduous trees to obtain a measure of availability. Trembling aspen was used much more often than in proportion to its availability, whereas the proportion of paper birch was lower among nest trees than within the random sample (Fig. 2). To further analyse differences between use and

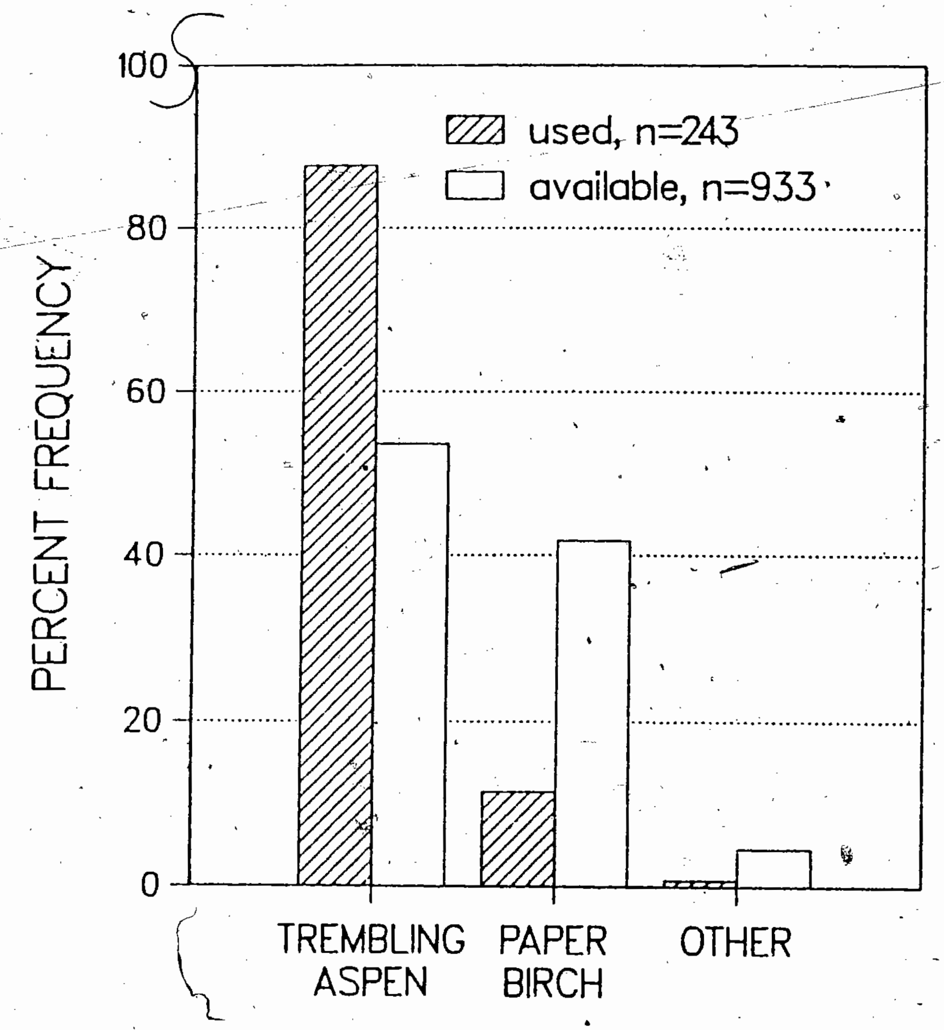

Fig. 2. Species of nest trees (used) and of trees in the random sample (available). Data for all species of primary cavity-nesting birds were pooled. "Other" tree species are black cottonwood, thin-leaved mountain alder and willow (*Salix* sp.).

availability, I calculated a linear index of selection developed by Strauss (1979), which is defined as: (% use − % availability)/100. Values for this index range from −1 to 1. An index of 0 indicates that a habitat component is used in proportion to its occurrence. Other more complex selection indices exist (see Lechowicz 1982 for a review) but this one satisfied the requirements of my study. I calculated 95% simultaneous confidence intervals for each index value. Trembling aspen was used more than in proportion to its availability by Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker, resulting in positive selection indices (Fig. 3). The positive indices mean that these birds prefer trembling aspen to paper birch and other tree species for nesting. Their indices for paper birch are negative, indicating avoidance. Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker also have positive indices for trembling aspen and negative indices for paper birch, but the confidence intervals include 0, so no significant preference or avoidance patterns can be concluded. Chi-square tests conducted for each bird species showed no significant difference between use and availability of tree species for Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker.

Wide confidence intervals such as those of Downy Woodpecker are due to small sample size. However, in cases where no nests were found, confidence intervals are narrow for each bird species, and do not reflect differences in sample size. Strauss' selection index must be viewed as a relative rather than absolute measure, i.e. the magnitude of the index is influenced by addition or removal of categories of the variable considered. Classification of a category as "preferred" or "avoided" may thereby change. The rank order of each category's index, however, remains unaffected (Johnson 1980).

Tree size

Mean diameter (at breast height, dbh) of nest trees ranged from 26 cm for Red-breasted Nuthatch and Downy Woodpecker to 40.5 cm for Pileated Woodpecker (Table 2). The mean value for Pileated Woodpecker was significantly larger than those of the other 5 species. Pileated Woodpecker did not nest in trees smaller than 25.8 cm dbh. The smallest

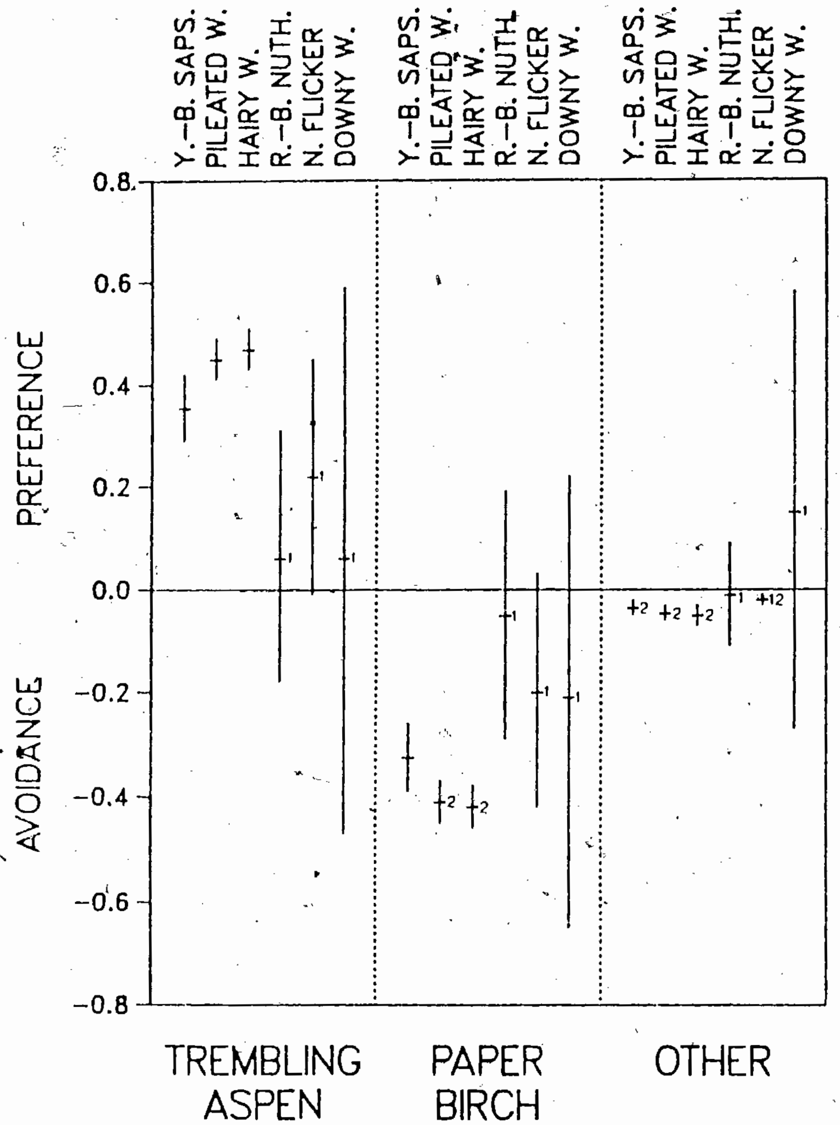

Fig. 3. Selection of tree species by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. "Other" tree species are black cottonwood, thin-leaved mountain alder, and willow. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test). Cases where no nests were found are marked with superscript "2".

Table 2. Diameter and height of trees used for nesting by primary cavity-nesting birds, and height of nest entrances. Mean values with the same letter are not significantly different (Duncan's Multiple Range Test).

Bird species	n	Nest tree diameter (cm dbh)			
		Mean	SE	Min.	Max.
Yellow-bellied Sapsucker	159	32.8A	0.6	20.1	60.8
Pileated Woodpecker	20	40.5B	1.6	25.8	57.3
Hairy Woodpecker	8	27.6AC	3.0	17.4	44.5
Red-breasted Nuthatch	24	26.4C	1.0	17.3	36.2
Northern Flicker	17	31.9AC	2.4	19.8	48.7
Downy Woodpecker	5	26.3AC	2.4	19.1	31.4
all species[1]	243	32.3	0.5	17.3	60.8
		Nest tree height (m)			
	n	Mean	SE	Min.	Max.
Yellow-bellied Sapsucker	159	18.4A	0.4	5.4	31.2
Pileated Woodpecker	20	19.2A	1.4	7.7	25.9
Hairy Woodpecker	8	18.3A	2.3	6.1	27.7
Red-breasted Nuthatch	24	12.1B	1.1	4.5	25.1
Northern Flicker	17	14.7BC	1.9	2.1	26.8
Downy Woodpecker	5	15.7AC	3.2	9.5	24.9
all species[1]	243	17.4	0.4	2.1	31.2
		Nest entrance height (m)			
	n	Mean	SE	Min.	Max.
Yellow-bellied Sapsucker	159	8.0A	0.3	1.3	19.6
Pileated Woodpecker	20	9.2A	0.4	6.8	12.6
Hairy Woodpecker	8	8.0AB	1.8	2.8	16.4
Red-breasted Nuthatch	24	8.7A	0.7	3.5	15.6
Northern Flicker	17	5.7B	0.9	1.6	12.2
Downy Woodpecker	5	8.9AB	1.0	5.8	11.2
all species[1]	243	7.9	0.3	1.3	19.6

[1]includes nests of unconfirmed species

nest trees, 17 cm in diameter, were occupied by Red-breasted Nuthatch and Hairy Woodpecker.

Comparison of use and availability, with all bird species pooled, showed that trees below the 25–29 cm dbh class were used less than in proportion to their availability, i.e. they were avoided (Fig. 4). Larger diameter classes were preferred. The same general pattern was observed for Yellow-bellied Sapsucker alone, because the nest sample was dominated by this species (Fig. 5). Pileated Woodpecker avoided trees below the diameter class 30–34 cm, and showed a strong preference for trees greater than 40 cm dbh. No consistent pattern was evident for Northern Flicker, which significantly avoided trees in the 15–19 cm and in the 25–29 cm diameter classes. The relatively strong, but not significant, preference of Northern Flicker for trees above 40 cm dbh is probably due to its use of old Pileated Woodpecker cavities. Use and availability did not differ significantly for Hairy Woodpecker, Red-breasted Nuthatch, and Downy Woodpecker. Reduction in the number of size classes considered would have accentuated preference and avoidance patterns where selection indices of joined size classes had the same sign. The diminished resolution, however, would have resulted in some loss of information.

Mean height of nest trees ranged from 12 m for Red-breasted Nuthatch to 19 m for Pileated Woodpecker (Table 2). Nest trees of Red-breasted Nuthatch had significantly lower mean heights than those of all other species except Northern Flicker. Mean values for Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker did not differ significantly and were greater than those of Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker, although this difference was not significant in the case of Downy Woodpecker which had a very small sample size. The shortest nest tree, 2 m in height, was occupied by Northern Flicker.

Results of selection analyses involving tree height are not shown because height was correlated with tree diameter and with top and tree condition. These correlations dominated selection patterns, masking any possible selection for tree height itself. Tall trees were

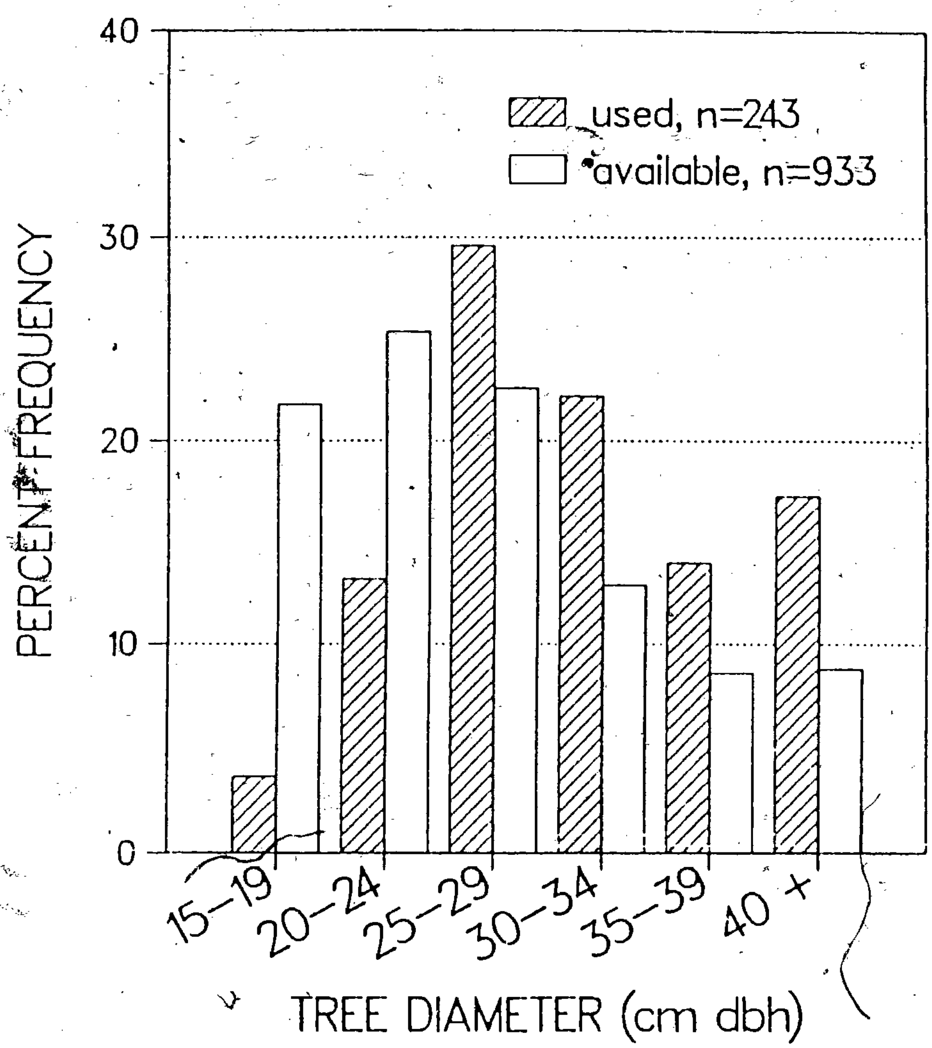

Fig. 4. Diameter classes of nest trees (used) and of trees in the random sample (available). Data for all species of primary cavity-nesting birds were pooled.

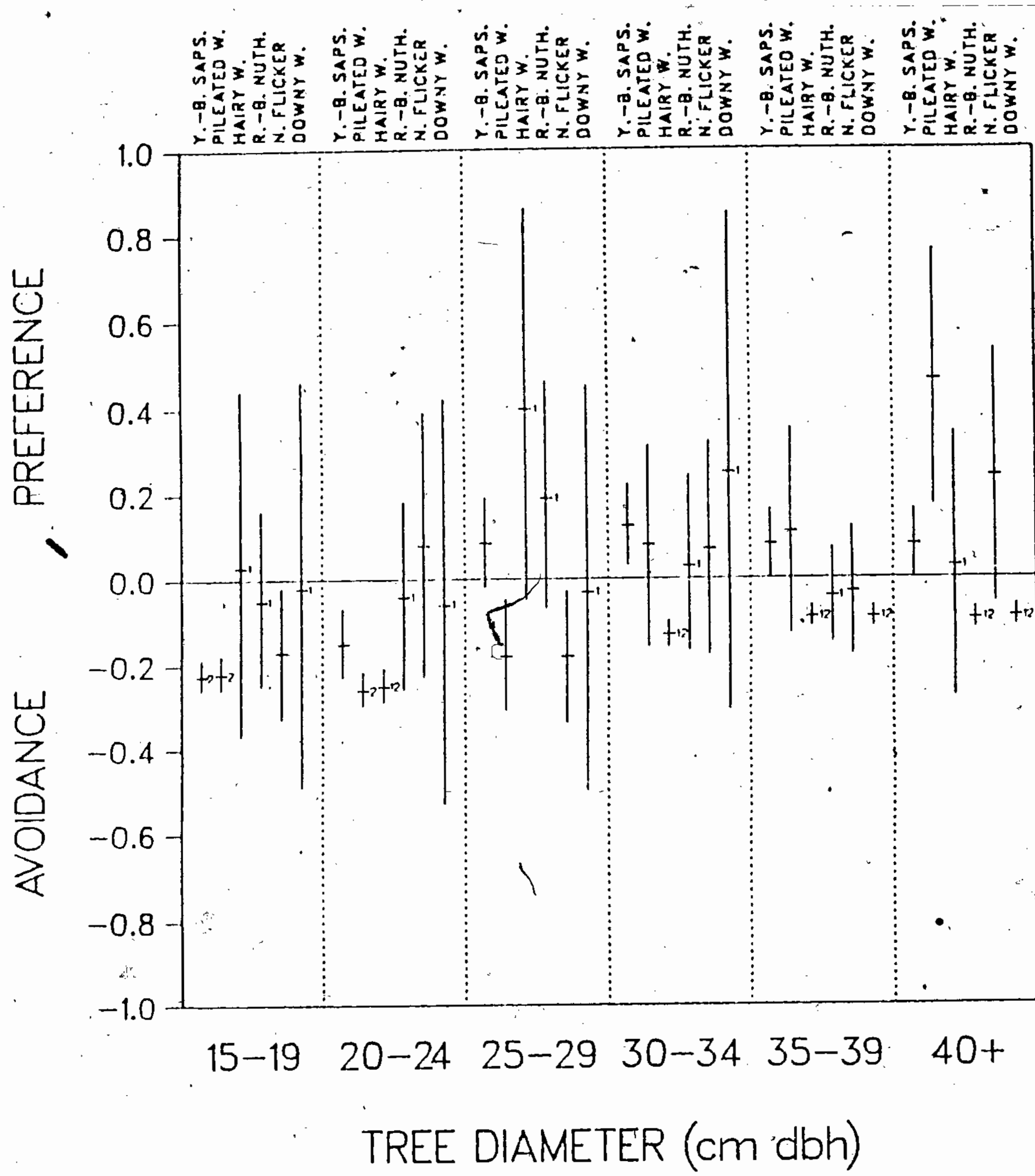

Fig. 5. Selection of tree diameter classes by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test). Cases where no nests were found are marked with superscript "2".

preferred because they tended to be in the larger diameter classes and short trees were preferred by some bird species because they tended to be dead or have dead tops. The selection pattern for tree height therefore displayed a misleading double peak in preference with an apparent avoidance of intermediate height classes.

Mean heights of nest cavity entrances ranged from 5.7 m for Northern Flicker to 9.2 m for Pileated Woodpecker. Except for Northern Flicker all species had very similar mean nest hole heights. The lowest nest found was located 1.3 m above the ground and was occupied by Yellow-bellied Sapsucker.

Tree condition

Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker used live trees with live tops more often than dead trees or trees with dead tops, whereas the opposite was found for Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker (Table 3).

Selection for tree condition differed markedly between trembling aspen and paper birch, hence the 2 tree species were examined separately. Dead trees and live trees with dead tops were treated as one category. Use and availability within each of the 2 tree condition categories were almost equal in trembling aspen, when bird species were pooled (Fig. 6). When species were considered separately, no significant difference between use and availability was found for Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker (Fig. 7). Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker, however, showed a significant preference for dead or partly dead trembling aspen. Live trees with live tops were avoided with the same magnitude, since for dichotomous variables, selection patterns in the 2 categories are mirror images of one another.

For paper birch, no nests were excavated in fully live trees (Fig. 8), which is reflected in the strong avoidance of this category by all bird species (Fig. 9). Sample sizes of nests in paper birch were only large enough to calculate selection indices for Yellow-bellied Sapsucker and Red-breasted Nuthatch.

Table 3. Condition of trees used for nesting by primary cavity-nesting birds.

Bird species	Number of nests found			
	Total	Dead	Live with dead top	Live with live top
Yellow-bellied Sapsucker	159	18	14	127
Pileated Woodpecker	20	6	2	12
Hairy Woodpecker	8	1	2	5
Red-breasted Nuthatch	24	10	9	5
Northern Flicker	17	8	4	5
Downy Woodpecker	5	4	1	-
all species[1]	243	49	33	161

[1]includes nests of unconfirmed species

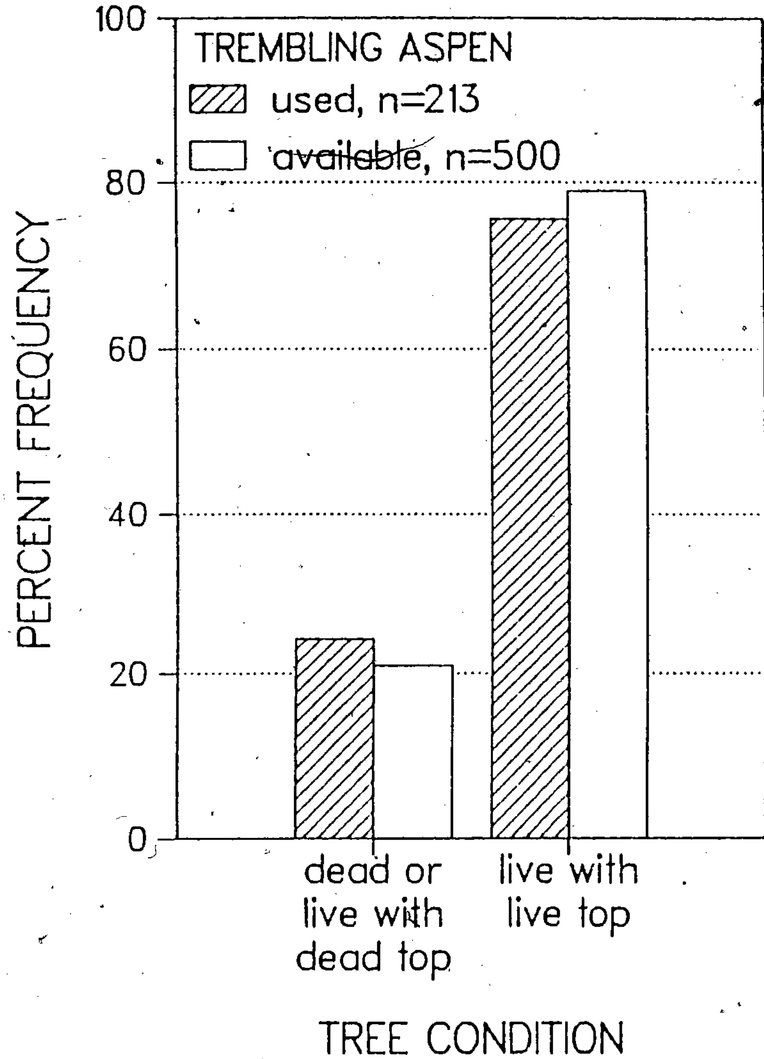

Fig. 6. Condition of nest trees (used) and of trees in the random sample (available), for trembling aspen. Data for all species of primary cavity-nesting birds were pooled.

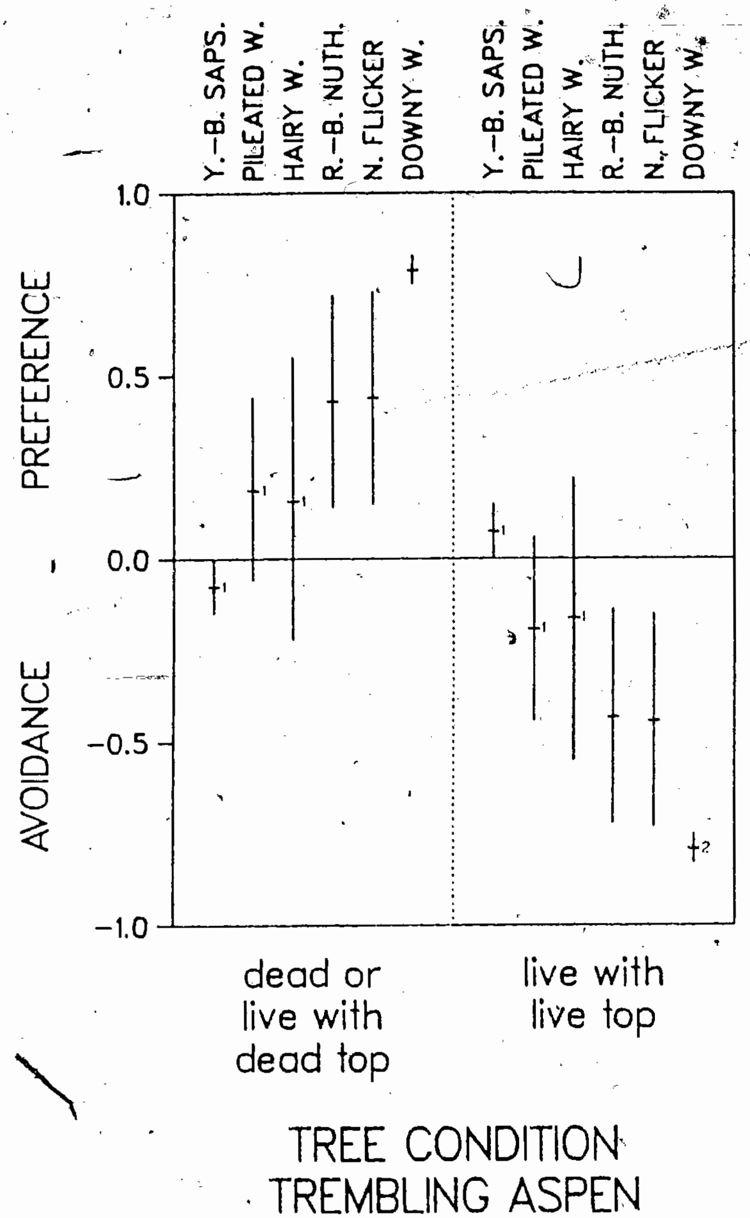

Fig. 7. Selection of tree conditions in trembling aspen by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test). Cases where no nests were found are marked with superscript "2".

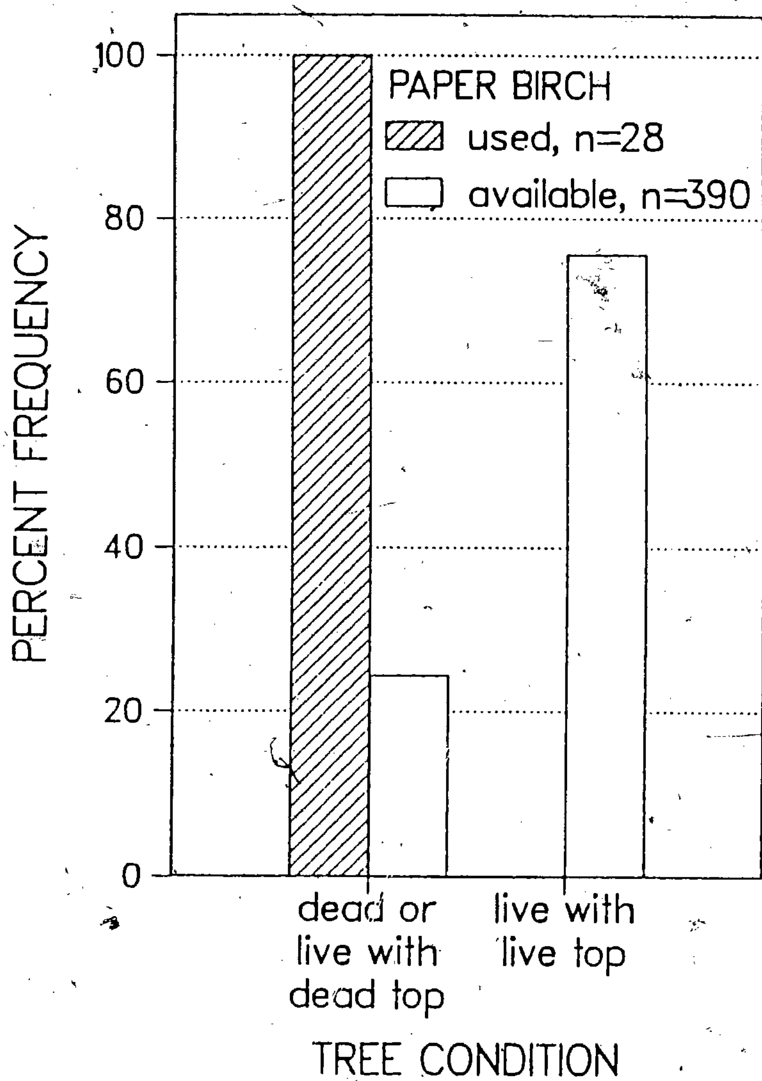

Fig. 8. Condition of nest trees (used) and of trees in the random sample (available), for paper birch. Data for all species of primary cavity-nesting birds were pooled.

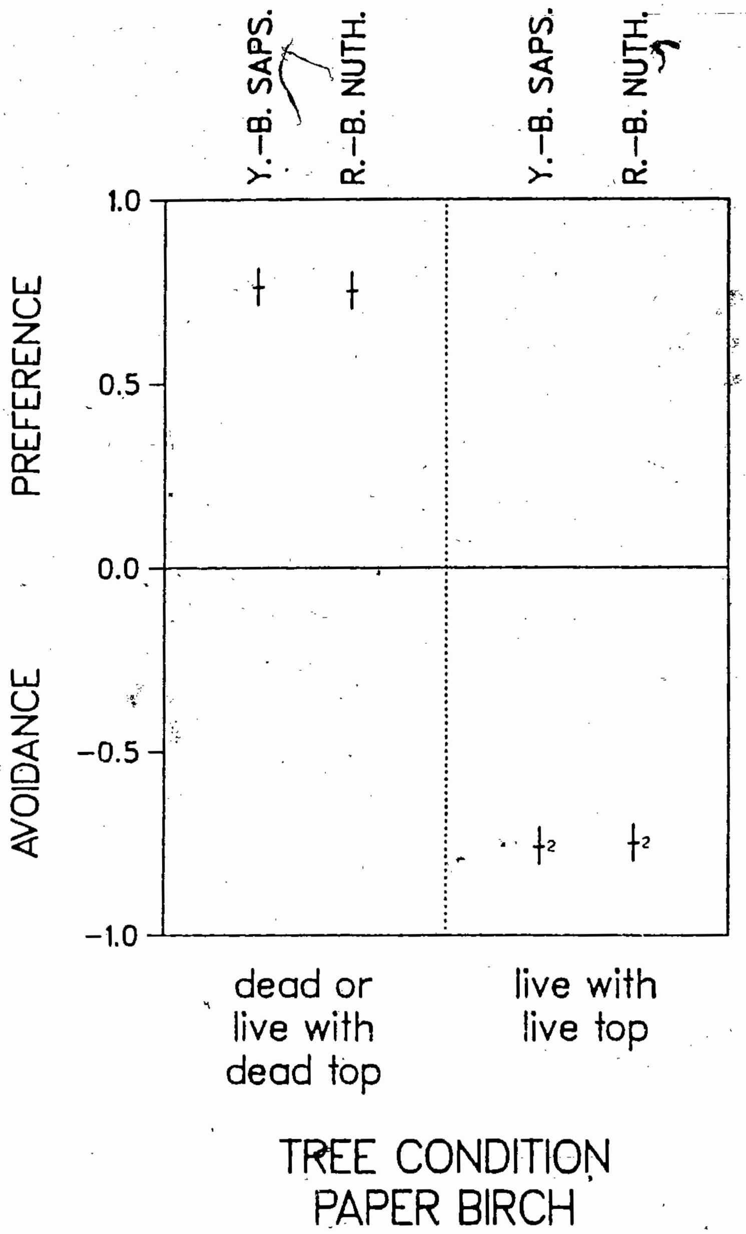

Fig. 9. Selection of tree conditions in paper birch by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test). Cases where no nests were found are marked with superscript "2".

Heartwood decay

All trees were examined for presence of the following indicators of heartwood decay: fungal fruiting bodies (conks), scars showing exposed wood, and broken tops. Fungal conks are a definite sign of decay, whereas scars or broken tops merely indicate that decay is likely to be present since they represent possible entrance points for heartwood decay organisms. All species except Pileated Woodpecker and Northern Flicker used trees with fungal conks more frequently than trees without conks (Table 4). Two species of fungus were identified. The most common one was *Fomes igniarius*, which occurred mainly on trembling aspen. The other species, *Fomes fomentarius*, was mostly associated with paper birch. Only 10% of available trees had fungal conks, whereas they were present on 70% of the nest trees (Fig. 10). A significant preference for nesting in trees bearing fungal conks was observed for all bird species (Fig. 11).

Use of trees with and without scars was quite similar, although the latter were used slightly more often by all bird species (Table 4). Comparison with availability showed that nesting use of trees with scars exceeded the proportion of scarred trees in the random sample (Fig. 12). When selection was examined for each bird species separately, however, only Yellow-bellied Sapsucker showed a significant preference for trees with evidence of past injury (Fig. 13). For all other species, Chi-square tests indicated no significant difference between use and availability.

In the analyses examining selection for top condition, I only considered dead trees or live trees with dead tops, because live trees with live tops, by definition, have intact tops. All species except Hairy Woodpecker, which was represented by only 3 nests, used trees with broken tops more often than those with intact tops (Table 4). Consideration of availability showed that trees with broken tops were used more than in proportion to their availability (Fig. 14). Excluding fully live trees, however, greatly reduced sample sizes, so that differences between use and availability were not significant (Fig. 15). Although all confidence intervals included 0, a tendency was apparent for all bird species to prefer trees with broken tops to

Table 4. Presence of decay indicators on nest trees used by primary cavity-nesting birds.

Bird species	n	Species of fungal conks				Scars		Top condition[1]	
		Fomes igniarius	*Fomes fomentarius*	not identified	no conks	present	absent	intact	broken
Yellow-bellied Sapsucker	159	112	7	5	35	78	81	14	18
Pileated Woodpecker	20	8	1	1	10	9	11	3	5
Hairy Woodpecker	8	5	-	-	3	3	5	3	-
Red-breasted Nuthatch	24	9	4	1	10	11	13	5	14
Northern Flicker	17	4	3	-	10	8	9	5	7
Downy Woodpecker	5	3	1	-	1	2	3	1	4
all species[2]	243	144	18	7	74	115	128	32	50

[1] includes only dead trees or live trees with dead tops
[2] includes nests of unconfirmed species

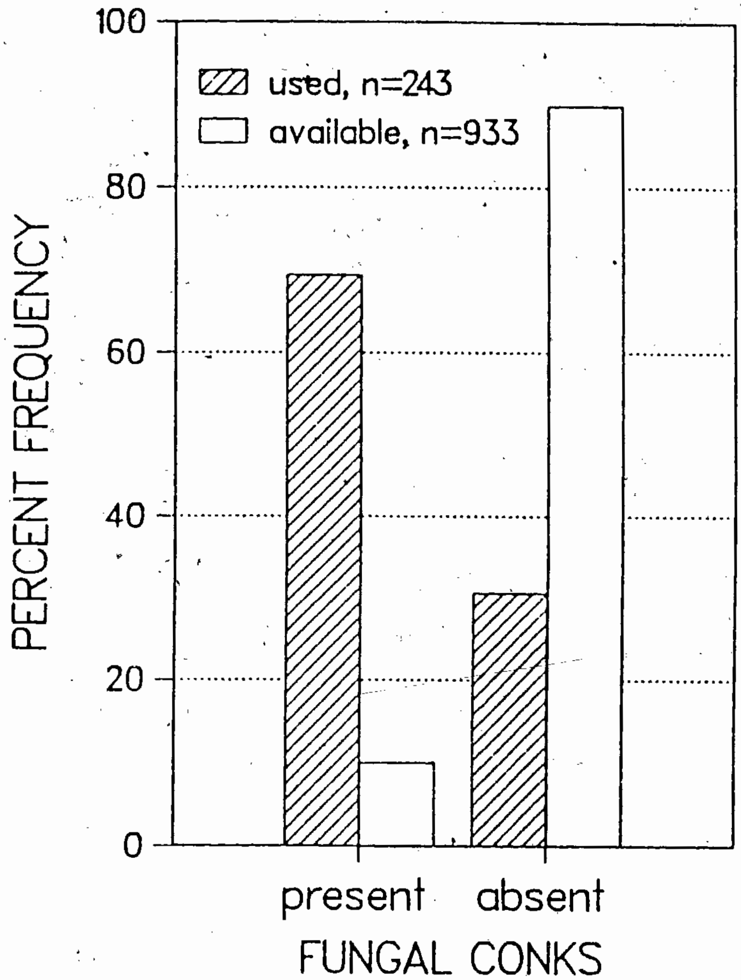

Fig. 10. Presence of fungal conks on nest trees (used) and of trees in the random sample (available). Data for all species of primary cavity-nesting birds were pooled.

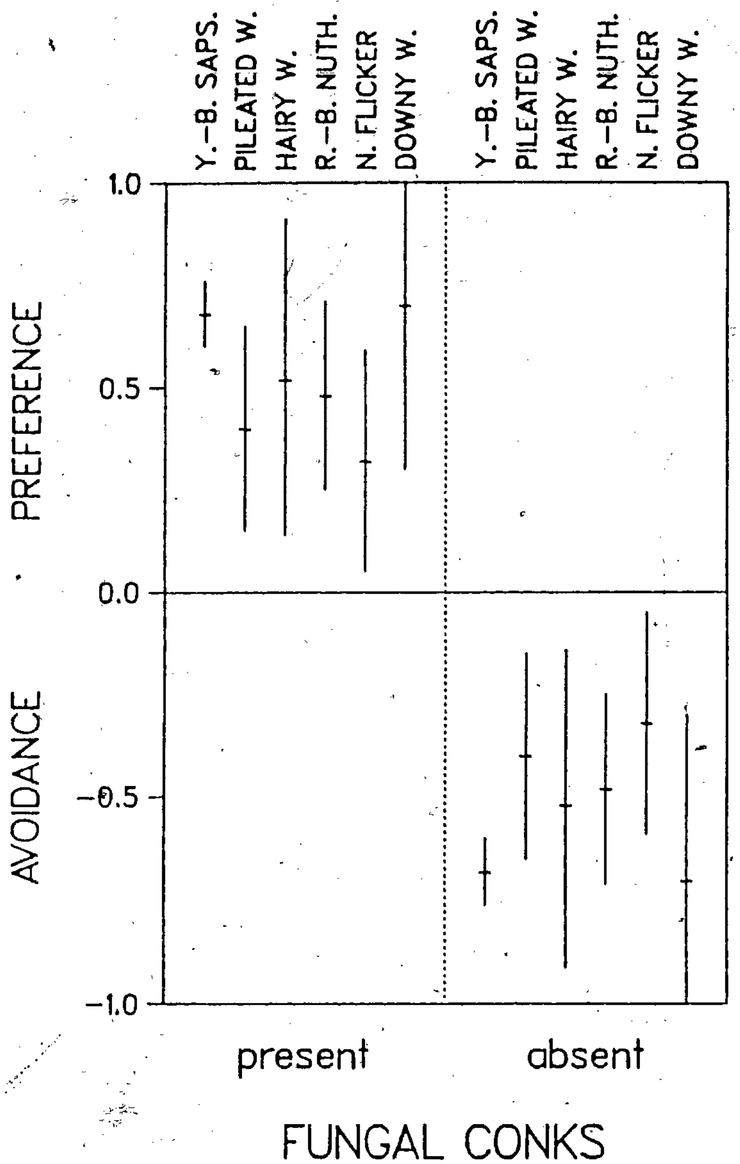

Fig. 11. Selection of trees with and without fungal conks by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1.

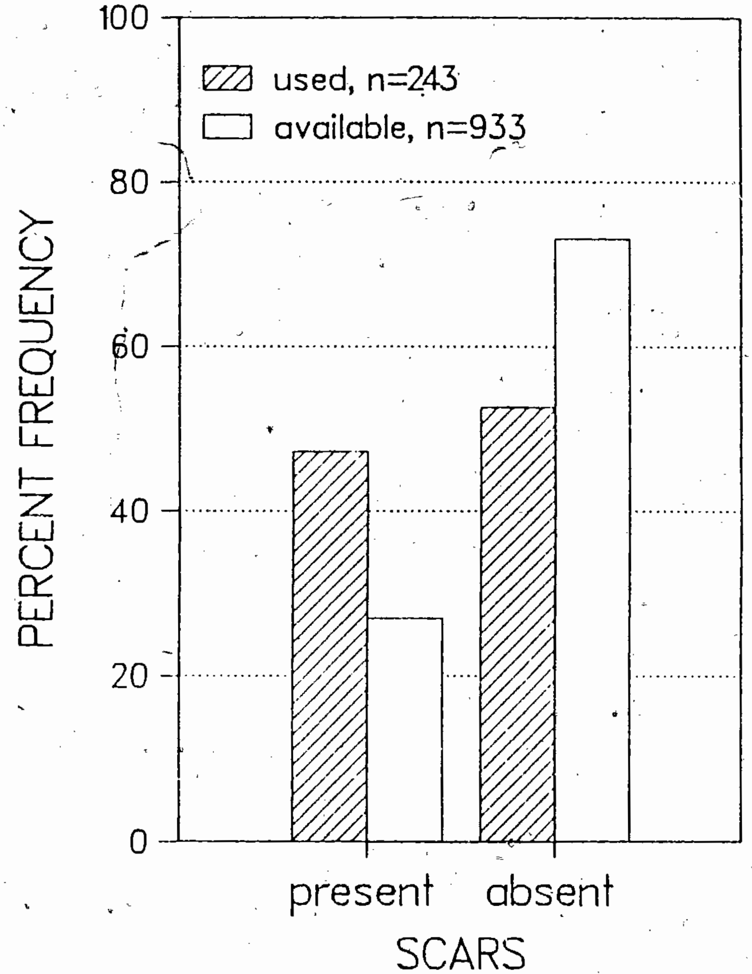

Fig. 12. Presence of scars on nest trees (used) and of trees in the random sample (available). Data for all species of primary cavity-nesting birds were pooled.

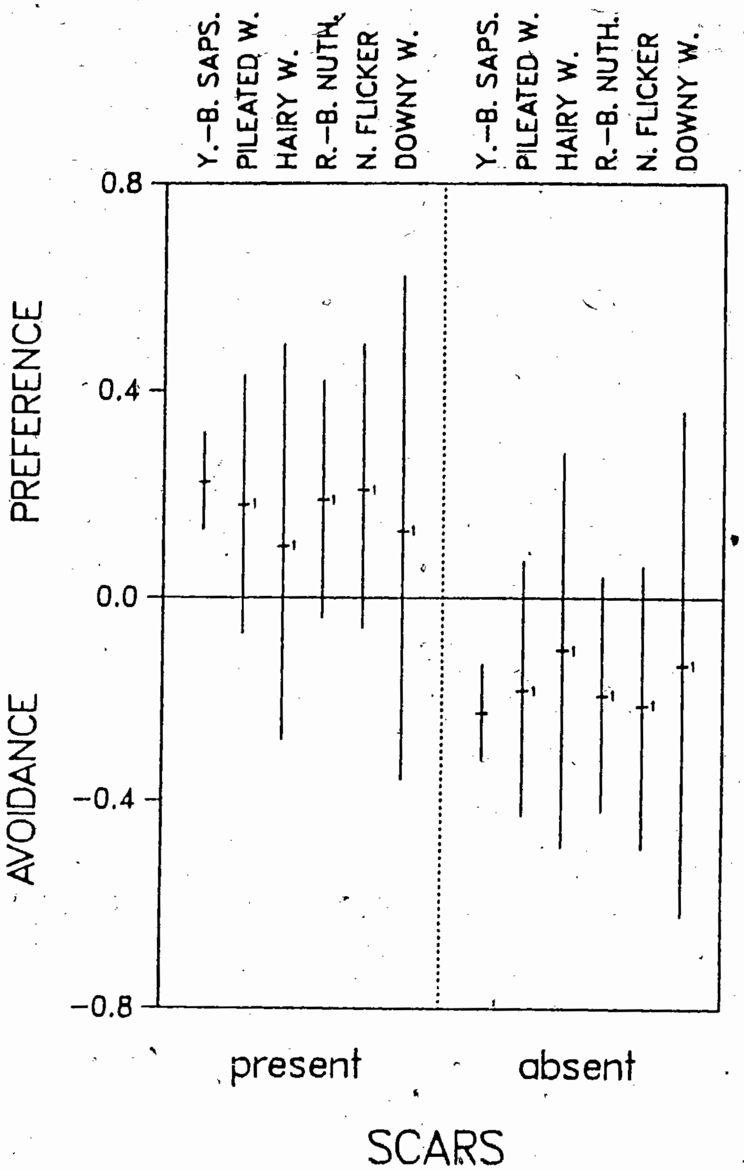

Fig. 13. Selection of trees with and without scars by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test).

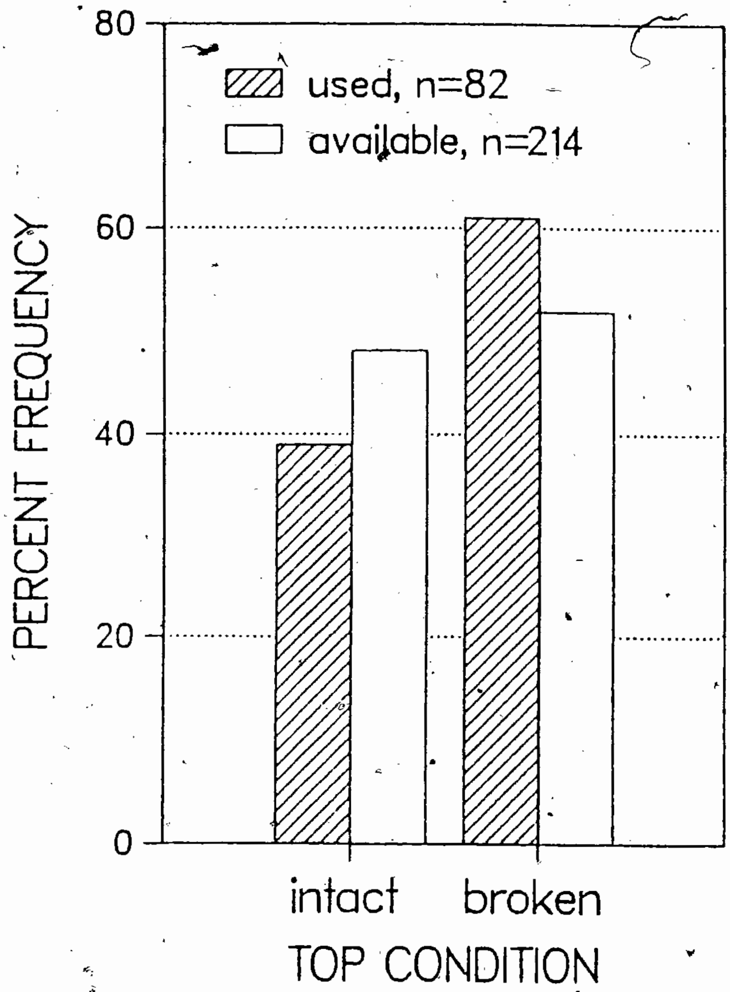

Fig. 14. Top condition of nest trees (used) and of trees in the random sample (available). Only dead trees and live trees with dead tops are considered. Data for all species of primary cavity-nesting birds were pooled.

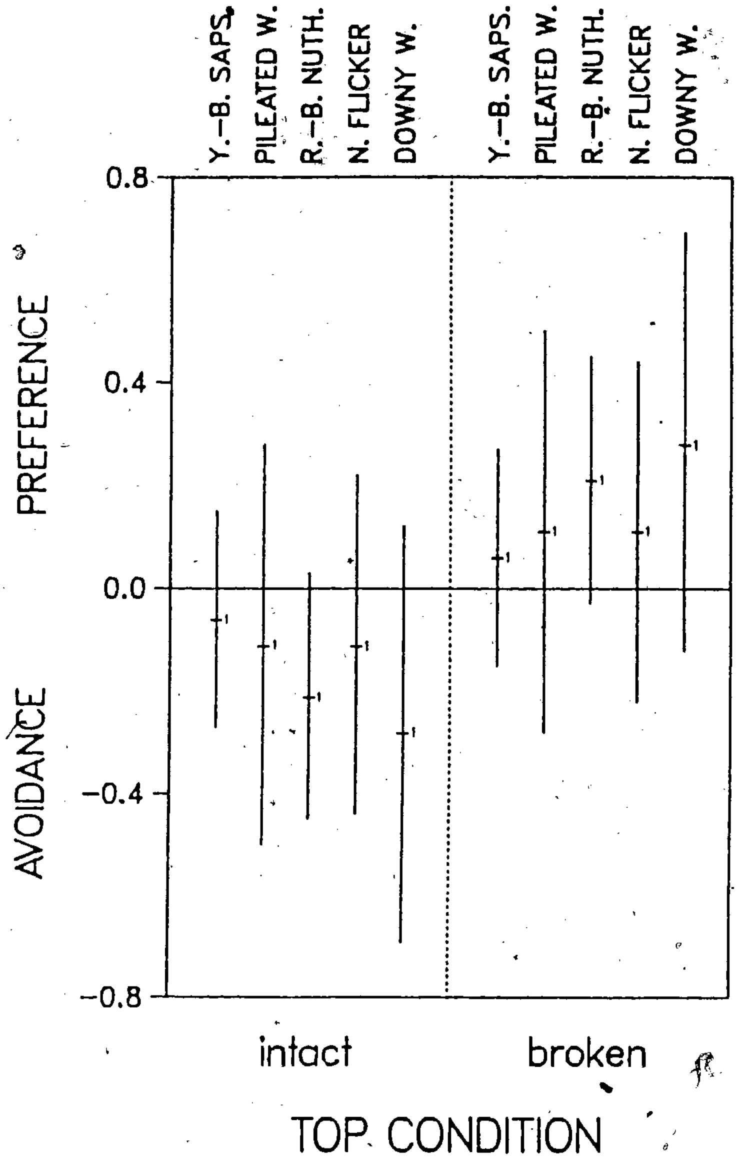

Fig. 15. Selection for top condition in dead trees or live trees with dead tops by primary cavity-nesting birds. Vertical lines represent 95% simultaneous confidence intervals. Complete bird names are listed in Table 1. Hairy Woodpecker was excluded from the analysis because only 3 nests were found in dead trees or trees with dead tops. A superscript "1" indicates that difference between use and availability was not significant (Chi-square test).

intact trees. This tendency was strongest in the cases of Red-breasted Nuthatch and Downy Woodpecker.

Nest Entrance Orientation

Observed nest entrance orientations were grouped into 8 compass directions (Fig. 16). I conducted a one-sample Chi-square test with equal expected frequencies for each of the 8 directions (Batschelet 1965), to test for preferences in entrance orientation. Although it appeared that nest entrances faced most often west and south-west, and least often north, no preference was detected, i.e. nest hole orientations did not significantly differ from uniform. The same result was obtained whether bird species were pooled or each species considered separately.

Comparison of Old Cavities and Active Nests

Active nests are often scarce and nest searches are time consuming. I repeated the selection analyses, based on the presence of old, unoccupied nest cavities, to determine whether old cavities could be used in studies of nest site selection to increase sample sizes of nests and efficiency of sampling. Of the nest and sample trees, 228 had one or more old cavities, that had been excavated by primary cavity-nesting birds. Old cavities were not subdivided by bird species because the excavator species could not be confirmed. Selection was calculated with the 228 trees containing old cavities representing nesting use. The sample of available trees was the same as in the selection analyses involving active nests. The pattern of selection based on old, unoccupied cavities was found to be very similar to that based on active nests with all bird species pooled (Table 5). The only exception to this similarity was the variable top condition. Active nests indicated a preference for broken tops, whereas selection indices based on old cavities showed a preference for intact tops. However, none of the selection indices for top condition were significant.

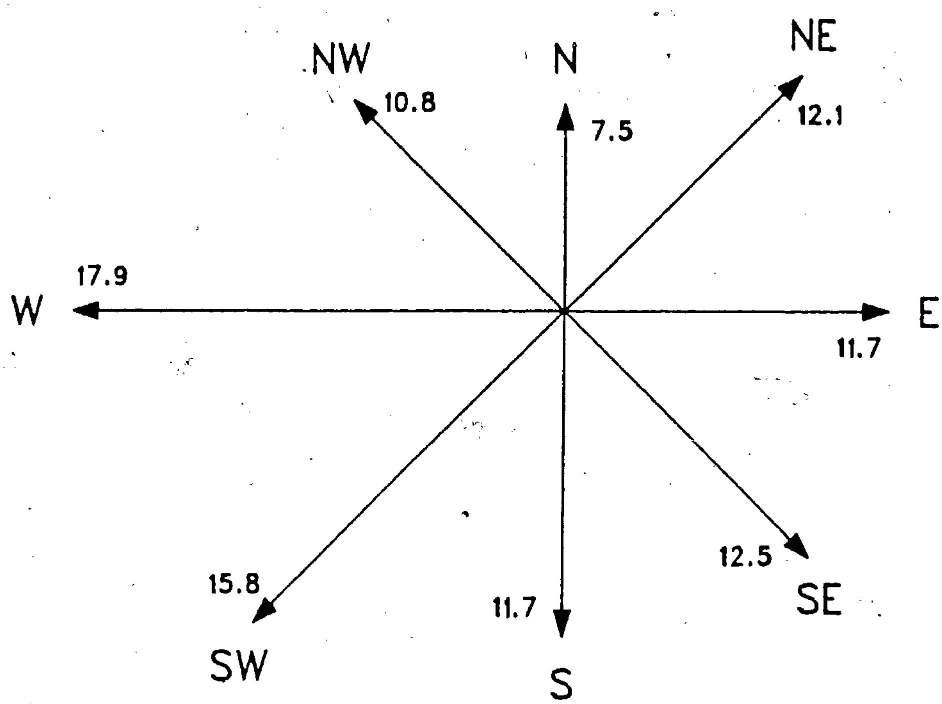

Fig. 16. Orientation of nest entrances, grouped into 8 compass directions. Lengths of arrows are proportional to numbers of nests represented. Numbers are percentages. Data for all species of primary-cavity-nesting birds were pooled.

Table 5. Comparison of nest tree selection indices based on active nests and on old, unoccupied cavities of primary cavity-nesting birds.

Variable	Selection indices ±95% simultaneous confidence intervals: Active nests (n=243)	Old, unoccupied cavities (n=228)
Tree species		
Trembling aspen	0.32±0.07	0.29±0.07
Paper birch	-0.29±0.06	-0.27±0.07
Other[1]	-0.03±0.02	-0.02±0.03
Tree diameter (cm dbh)		
15-19	-0.19±0.05	-0.18±0.05
20-24	-0.13±0.07	-0.12±0.07
25-29	0.06±0.09	0.02±0.08
30-34	0.10±0.08	0.13±0.08
35-39	0.05±0.07	0.06±0.07
≥40	0.09±0.07	0.09±0.06
Tree condition		
Trembling aspen		
dead or dead top	0.04±0.08	0.05±0.08[2]
live with live top	-0.04±0.08	-0.05±0.08[2]
Paper birch		
dead or dead top	0.76±0.06	0.73±0.09
live with live top	0.76±0.06	-0.73±0.09
Fungal conks		
present	0.60±0.07	0.52±0.08
absent	-0.60±0.07	-0.52±0.08
Scars		
present	0.21±0.08	0.22±0.08
absent	-0.21±0.08	-0.22±0.08
Top condition[3]		
intact	-0.09±0.14[2]	0.14±0.15[2]
broken	0.09±0.14[2]	-0.14±0.15[2]

[1]includes black cottonwood, thin-leaved mountain alder, and willow

[2]difference between use and availability not significant (Chi-square test)

[3]includes only dead trees or live trees with dead tops

Nest Tree Variation among Species of Primary Cavity-Nesting Birds

Most of the variables describing nest tree characteristics showed some degree of intercorrelation. I conducted a principal components analysis to obtain independent linear combinations of the original variables that summarize most of the variation in the data on nest tree use. The analysis was based on 7 tree variables (Table 6). Only trembling aspen and paper birch, which contained all but 2 of the nests found, were considered, so tree species could be treated as a dichotomous variable. Nests of Red-breasted Nuthatch and Northern Flicker in old cavities excavated by other species were excluded to obtain a more accurate characterization of trees used by each species for building their own nest cavities.

Four of the components extracted each explained more than 10% of the total variance (Table 6). Together they accounted for 81.9% of the variation in the data set. The direction and relative strengths of correlations between principal component axes and original variables were used for a biological interpretation of each component. The first principal component mainly summarized a correlated complex of variables represented by tree height and condition of tree and top. High scores on this first axis indicate short dead nest trees with broken tops, whereas low values characterize nest trees that are tall, live and have intact tops. The second component is less interpretable. Although presence of fungal conks, tree diameter, and tree species are most highly correlated with this component, the correlations coefficients of all other variables, except tree height ,are also strong. The third axis shows a clear correlation with presence of scars, and presence of fungal conks characterizes the fourth principal component. The second, third, and fourth components may not be particularly meaningful combinations of variables, because biologically interpretable combinations are not necessarily orthogonal (mutually perpendicular), as are the axes constructed in the principal components analysis (Neff and Marcus 1980).

Mean scores of each bird species along the first and second principal component axes were plotted for visual examination of nest tree similarities and differences. The 2-dimensional space formed, contained 56.6% of the total variation (Fig. 17). Yellow-bellied Sapsucker,

Table 6. Results of principal components analysis of 7 nest tree variables for 6 species of primary cavity-nesting birds. Only components explaining more than 10% of the variance are shown.

	Principal component			
	I	II	III	IV
Variance explained (%)	35.1	21.5	13.9	11.4
Cumulative variance explained (%)	35.1	56.6	70.5	81.9
Correlations between components and original variables				
Tree species[1]	0.47	-0.50	0.30	0.34
Tree diameter (cm dbh)	-0.54	0.60	0.01	-0.22
Tree height (m)	-0.87	0.09	-0.03	-0.02
Tree condition[1]	0.76	0.41	-0.12	-0.22
Presence of fungal conks[1]	0.02	0.65	-0.17	0.74
Presence of scars[1]	-0.02	0.36	0.91	-0.02
Top condition[1]	0.78	0.40	-0.05	-0.18

[1]Dichotomous variables are coded as 0 and 1, where 0 denotes trembling aspen, live with live top, absence of fungal conks, absence of scars, and intact top.

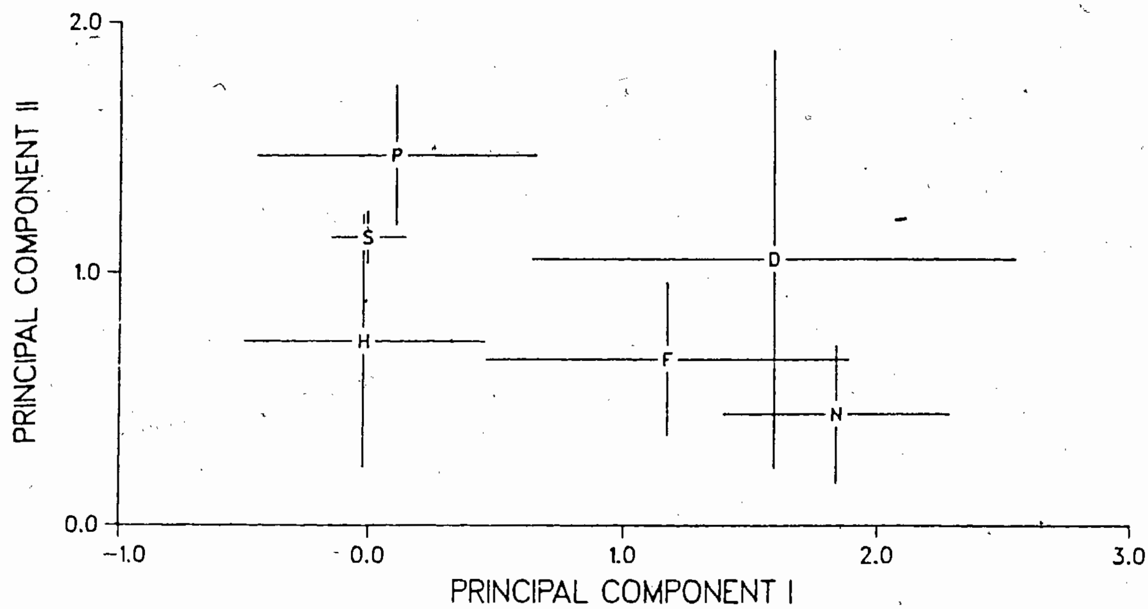

Fig. 17. Mean scores ± 2 standard errors for nest trees of 6 species of primary cavity-nesting birds along the first and second principal component axes. Letter codes are centred on species' mean scores. See Table 6 for contributions of original nest tree variables to each principal component. Nests of Red-breasted Nuthatch and Northern Flicker in old cavities built by other species were excluded. S=Yellow-bellied Sapsucker (n=159), P=Pileated Woodpecker (n=20), H=Hairy Woodpecker (n=8), N=Red-breasted Nuthatch (n=17), F=Northern Flicker (n=14), D=Downy Woodpecker (n=4).

Pileated Woodpecker, and Hairy Woodpecker had very similar scores along the first axis and were well separated from Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker. Species in the latter group assumed higher values because they nested more frequently in dead or broken trees which were on average shorter than nest trees of Yellow-bellied Sapsucker, Pileated Woodpecker, or Hairy Woodpecker. Red-breasted Nuthatch had the highest mean score. Although small sample sizes of some species, especially Downy Woodpecker, resulted in wide confidence intervals, the 2 groups formed along the first axis remained distinct. There was much less separation of species along the second principal component axis. The highest mean score on this axis was for Pileated Woodpecker, which on average used larger nest trees than any other species and nested exclusively in trembling aspen. The mean score of Pileated Woodpecker was significantly different from the means of Northern Flicker and Red-breasted Nuthatch. Yellow-bellied Sapsucker also had a significantly higher mean score than Northern Flicker and Red-breasted Nuthatch, because nest trees of Yellow-bellied Sapsucker were generally larger, had a high incidence of fungal conks, and nests were mainly in trembling aspen.

Relative Value of Tree Characteristics as Indicators of Nest Tree Suitability

A stepwise logistic regression was conducted for trembling aspen, in which the characteristics of nest trees and of non-nest trees were analysed to determine which variables most accurately predicted the probability of an active nest being present or absent in a given tree. The best predictors were considered to be the most reliable indicators of a tree's quality as nest site for primary cavity-nesting birds. Of the 6 tree variables tested, tree condition and height did not achieve the F-value required to enter the model. All other variables significantly improved the model upon their addition and can thus be considered good predictors of nest presence or absence (Table 7). However, presence of fungal conks was entered first and its improvement Chi-square value far exceeded those of all other variables. Presence of conks is thus the best indicator of a tree's quality as nest site for

Table 7. Summary of stepwise logistic regression for trembling aspen, analyzing characteristics of nest trees and trees without nests. Species of primary cavity-nesting birds were combined in the analysis.

Variable	Step entered	Improvement Chi-square	P value
Presence of fungal conks	1	279.7	0.00
Presence of scars	2	29.8	0.00
Top condition	3	15.7	0.00
Tree diameter[1]	4	16.2	0.00
Tree condition	not entered		
Tree height[1]	not entered		

[1] $\log_e$ transformed

primary cavity-nesting birds. The next best variables to be used in conjunction with presence of conks for further improving the predictive power of the model, were presence of scars and top condition. Bird species were pooled for this analysis to obtain a sufficiently large sample size. Since the nest sample was dominated by Yellow-bellied Sapsucker, results were mainly relevant to this species. Patterns for other bird species, which were not well represented in the pool of data, could therefore be different. Analyses based only on paper birch are not presented because the number of nests was too small to produce reliable results. However, it appeared that presence of fungal conks was also the best indicator of nest tree quality in paper birch.

Influence of Surrounding Vegetation on Nest Tree Selection

All nests were found in stands containing deciduous trees. These patches of deciduous or mixed forest comprised only 5% of the whole study area and thus appeared to be highly preferred for nesting compared to the surrounding coniferous forest, which consisted mainly of Douglas-fir.

I analysed a large number of parameters describing the vegetation surrounding each nest tree, within an 8 m radius (page 9), to determine whether characteristics of the vegetation in the immediate vicinity of a tree influenced whether the tree was chosen for nesting by primary cavity-nesting birds. The same variables were assessed for the immediate vicinity of randomly sampled trees to determine availability. To detect differences between the surroundings of used and available trees, I conducted Chi-square tests for each variable, considering each bird species separately. I then calculated Strauss' (1979) index of selection to examine patterns of preference and avoidance. Only 7 of the variables showed a significant difference between use and availability for some of the bird species. Almost all of the indices included 0, indicating that "selection" was not significantly different from random. The only significant selection patterns were avoidance by Pileated Woodpecker of nest trees surrounded by vegetation devoid of tall live trees, and avoidance by Yellow-bellied Sapsucker of nest trees in deciduous stands lacking trembling aspen. I therefore conclude that nest tree selection is guided by characteristics of the trees themselves and not by characteristics of the vegetation in the immediate vicinity, with the few exceptions outlined above.

CHAPTER V

DISCUSSION

Nest Tree Selection

Tree condition and decay

All species of primary cavity-nesting birds strongly preferred to nest in trees bearing fruiting bodies (conks) of heartwood rot fungi. Presence of fungal conks was the best indicator of a tree's quality as nest site, followed, at least in the case of trembling aspen, by 2 other indicators of heartwood decay (presence of scars and top condition). Heartwood decay thus appears to be the most important tree characteristic influencing selection of nest trees.

The species of decay agents involved in my study were in almost all cases the heartrot fungi *Fomes igniarius* in trembling aspen and *F. fomentarius* in paper birch (Riley 1952, Shigo 1965, Foster and Wallis 1974). *F. igniarius* invades live trees, softening the heartwood, while the sapwood remains unaffected. Such trees may be especially suitable as nest trees because the decayed heartwood is soft enough for easy excavation, and the hard shell of sound sapwood surrounds and protects the nest cavity (Shigo and Kilham 1968, Kilham 1971, Conner et al. 1976, Miller and Miller 1980). Most species of primary cavity-nesters are able to excavate the cavity entrance through sound wood. However, further inside the cavity, pecking movements are restricted and their blows have less force. Decayed wood is therefore required in the interior of the tree to construct the nest chamber (Miller and Miller 1980). Primary cavity-nesting birds can apparently locate, by sounding, portions along the tree trunk that have decayed heartwood, even if it is surrounded by healthy sapwood (Conner et al. 1976, Miller and Miller 1980).

Trees with fungal conks were also preferred in paper birch. However, the type of decay found in trembling aspen infected with *F. igniarius* does not usually occur, because the heartrot fungus associated with paper birch, *F. fomentarius*, appears to attack only dead trees or dead portions of live trees (Foster and Wallis 1974, personal observation). Live parts of paper birch therefore tend to have sound heartwood, which may explain the absence of nest cavities from live tree portions, which was also observed by McClelland and Frissell (1975). After tree death, the sapwood usually decays relatively fast in paper birch, so it soon loses its value as a protective shell.

Species of primary cavity-nesters have different capabilities with respect to the hardness of wood they can penetrate (Spring 1965). Yellow-bellied Sapsucker, Pileated Woodpecker and Hairy Woodpecker preferred to nest in trembling aspen with decayed heartwood surrounded by sound sapwood. They used dead and live trees without significant preference for either condition, probably because in trembling aspen the sapwood remains firm for some years after tree death, providing protection to the nest cavity (Reynolds et al. 1985, personal observation). Red-breasted Nuthatch and Downy Woodpecker, on the other hand, appeared unable to excavate through a hard sapwood shell. All self-excavated nests of these species were in dead trees or dead portions of live trees, which are likely to have both sapwood and heartwood softened by decay. Northern Flicker also preferred dead or partly dead trees for nesting. Five of the 14 apparently self-excavated nests of Northern Flicker were in live parts of trees. However, there were some indications that they may have been enlarged cavity attempts abandoned by Pileated Woodpecker. This affinity of Red-breasted Nuthatch, Northern Flicker and Downy Woodpecker for dead wood has also been observed in other studies (Lawrence 1967, Conner et al. 1975, Conner and Adkisson 1976, Raphael and White 1984, Madsen 1985). Lacking a firm shell, these nest sites offer less protection, but I noticed no signs of predation.

The division of the species of primary cavity-nesting birds into 2 groups was clearly shown in the principal components analysis, where Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker were separated from Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker along the first principal component axis. This axis was mainly characterized by tree condition and correlated variables (top condition and tree height), and may be interpreted as expressing the condition of the sapwood (live or dead). Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker were able to use live trees with heartwood decay, surrounded by sound sapwood. This group of species may be called "strong excavators", in contrast to the "weak excavators" Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker, which generally did not excavate through sound wood but appeared to require trees where decay had softened both sapwood and heartwood.

Presence of fungal conks is a definite sign of heartwood decay. An absence of fungal conks, however, does not necessarily mean that decay is not present, because decay fungi often do not produce fruiting bodies until years after initial infection. Two indirect decay indicators were included in the analyses: presence of scars with exposed wood, and top condition. Except for Yellow-bellied Sapsucker, primary cavity-nesting birds did not significantly prefer trees with scars for nesting. Scars were often basal, caused by logging machinery, and decay organisms may have have entered through the wound, but decay had not extended to a height acceptable for nesting.

Many investigators noted a preference for trees with broken tops (Conner and Adkisson 1976, Bull and Meslow 1977, McClelland 1977, McClelland 1979, Mannan et al. 1980, Scott et al. 1980, Harris 1983, Madsen 1985). A broken top probably accelerates invasion by heartrot fungi and the resulting decay occurs within a height range suitable for nesting. However, in my study, no significant selection for top condition was observed, although there appeared to be a tendency to prefer trees with broken tops. This absence of significant selection may have been partly due to the small sample size caused by exclusion of live trees from the analysis. Another possible reason why broken tops were not significantly preferred over intact tops and why most species did not select for scarred trees, is that, in the case of trembling aspen, decay organisms probably enter through dead branches and minor wounds (Conner et al. 1976, Anderson et al. 1977, Perala 1977, Etheridge and Hunt 1978, Scott et al. 1980), so that infection with heartrot fungi is common without top breakage or major injuries. Death of branches below the tree crown seemed to be part of the normal growth pattern for trembling aspen, providing an abundance of possible entrance points for decay organisms. Trembling aspen thus appears very prone to infection with heartrot fungi (Basham 1958). In paper birch, top breakage was usually subsequent to top death and softening of the wood by decay. In many cases, top death and decay may have been caused by sap-feeding Yellow-bellied Sapsucker, whose drill holes girdled the bole and facilitated entrance of fungal spores.

Importance of heartwood decay to primary cavity-nesters has been noted in many studies, involving various tree species. Preference of Yellow-bellied Sapsucker for trembling aspen infected with *F. igniarius* was reported by Lawrence (1967), Shigo and Kilham (1968), Kilham (1971), Erskine and McLaren (1972), Winternitz (1980), Scott et al. (1980), and Winternitz and Cahn (1983). In their study of Williamson's Sapsucker (*Sphyrapicus thyroideus*) and Red-naped Sapsucker (*Sphyrapicus* [*varius*] *nuchalis*), Crockett and Hadow (1975) found that both species preferred trembling aspen infected with *F. igniarius*. McClelland (1977) found that primary cavity-nesters preferred to nest in live or dead western larch (*Larix occidentalis*) with broken tops, infected with the heartrot fungi, *F. laracis* or *F. pini*; and also nested in broken top paper birch infected with *F. igniarius* or *F. fomentarius*. Nesting use of live western larch bearing conks of *F. laracis* was also observed by Madsen (1985). Ligon (1970) noted a dependence of the Red-cockaded Woodpecker (*Picoides borealis*) on living pines affected with *F. pini* heartrot and Kilham (1971) observed that Hairy Woodpeckers usually nest in trees infected with *F. igniarius*. Miller and Miller (1980) sectioned a large number of nest trees and found that almost all nests had been excavated in decayed wood. Conner et al. (1976), working in oak-hickory forests in southwestern Virginia, cultured wood samples from the heartwood of nest trees of Northern Flicker, Hairy, Downy, and Pileated Woodpeckers. They determined that all had been infected with heartrots prior to excavation. Several studies reported that Pileated Woodpecker can nest in sound wood (McClelland 1979, Miller and Miller 1980, Harris 1983). Harris (1983) ranked tree species according to wood hardness (based on specific gravity) and observed that in the species with the softest wood, decay may not be necessary to allow nest excavation. For weaker excavators than Pileated Woodpecker, however, all tree species may be too hard to excavate without the aid of decay.

My results and other studies indicate that presence of decayed heartwood is required by virtually all species of primary cavity–nesting birds for nest hole excavation, and is important in almost all tree species studied. Selection for tree condition and top condition, on the other hand, appears to vary among tree species, and seems to depend mainly on characteristics of the decay fungi associated with each tree species. Preference for tree condition also varies among bird species, according to their strength as excavators.

Tree size

A nest tree must have a large enough diameter to accommodate a cavity with room for an adult bird and nestlings. Species with larger body size obviously require nest trees with greater diameter than smaller species. Mean and minimum diameter of trees actually used for nesting usually exceed dimensions dictated by minimum space requirements. Possible advantages of nesting in larger trees are that cavities can have thicker walls which provide insulation, protection from predators, and lessen the danger of the nest trees breaking at cavity height (O'Connor 1978, Miller and Miller 1980, Raphael and White 1984). Studies of hole–nesting passerines in nest boxes have shown that clutch size increased with nest box area (Löhrl 1973, Karlsson and Nilsson 1977, Löhrl 1980, Trillmich and Hudde 1984). It is possible that there is a similar relationship for primary cavity–nesting birds. Use of larger nest trees, which can hold more spaceous cavities, may thus result in increased clutch size and nesting success. Hinds and Wengert (1977) noted a strong relationship between tree age and incidence of decay in trembling aspen in Colorado. This finding suggests that, in trembling aspen and other species where nests occur in live trees, larger trees, which are usually older, may be used because they are more likely to contain the decayed heartwood required for nest excavation. However, I found only a weak correlation between tree diameter and presence of fungal conks. The same observation was made by Winternitz and Cahn

(1983), for trembling aspen infected with *F. igniarius*. The reason may be that in trembling aspen, older trees, which are often decayed, can vary greatly in diameter among sites and clones.

In my study, Yellow-bellied Sapsucker avoided trees below the 25–29 cm diameter class and significantly preferred trees in the class 30–34 cm dbh. Preference did not rise with further increase in diameter, suggesting that there were no added advantages conferred by nesting in trees larger than 30–34 cm dbh. Selection indices for Red-breasted Nuthatch and Downy Woodpecker actually tended to decline in the larger diameter classes. This decline implies some disadvantage of larger trees, which may be explained by my observation that only a small proportion of trees in the large diameter classes were dead with the softened sapwood that these species need for cavity construction.

Mean and minimum diameters of nest trees in my study were much smaller than many of those reported in the literature (Kelleher 1963, Conner et al. 1975, McClelland and Frissell 1975, Bull and Meslow 1977, McClelland 1977, Scott 1978, McClelland 1979, Thomas 1979, Mannan et al. 1980, Scott et al. 1980, Raphael and White 1984, Bunnell and Allaye-Chan 1984, Madsen 1985, Zarnowitz and Manuwal 1985). The main reasons are probably that trembling aspen and paper birch never grow as large as some of the nest tree species in other areas, and that especially trembling aspen are favourable, safe nest sites because of the pattern of decay (softened heartwood surrounded by hard sapwood), in spite of their relatively small diameter compared to nest trees in other areas. Studies of nests in trembling aspen (Kilham 1971, Erskine and McLaren 1972, Crockett and Hadow 1975, Scott et al. 1980, Winternitz and Cahn 1983) showed nest tree diameters similar to those observed for trembling aspen in my study. Mean tree diameters used by primary cavity-nesting birds for nesting and preferred tree sizes thus appear to vary with tree species, partly because of differences in decay characteristics. It should not be assumed that the small diameters of trembling aspen and paper birch used for nesting would also be adequate in the case of other tree species.

Taller nest trees offer greater protection from predators, because nests can be placed higher above the ground (Kilham 1971, Dunn 1977, Nilsson 1984). Nest trees of Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker had greater mean heights than those of Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker. This height difference is due to the preference of the latter group of species for dead trees, which tend to be shorter because of broken tops or reduced crown height. I did not assess preference for tree height because of the strong correlation of this variable with top and tree condition. It appeared to be the least reliable indicator of nest tree quality (Table 7). In other studies, tree height seemed to be more important in nest tree selection (Raphaël and White 1984, Madsen 1985).

Tree species

In my study area, primary cavity-nesting birds nested only in trembling aspen, paper birch, and thin-leaved mountain alder. Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker, capable of penetrating a sound sapwood shell, preferred to nest in trembling aspen, which provided safe nest sites because of its decay characteristics. Red-breasted Nuthatch, Northern Flicker, and Downy Woodpecker used tree species in proportion to their occurrence. They appear to be weaker excavators and tree species does not seem to be important in their nest tree selection, as long as sapwood and heartwood are decayed enough for easy excavation.

Preference for nesting in trembling aspen has been reported in a number of other studies. Williamson's Sapsucker, Yellow-bellied Sapsucker, and Hairy Woodpecker preferred trembling aspen in ponderosa pine dominated and in trembling aspen dominated forest types in Arizona (Scott et al. 1980). Williamson's and Red-naped Sapsuckers, Hairy Woodpecker, Northern Flicker, and Downy Woodpecker preferred trembling aspen over a variety of coniferous species including ponderosa pine, Douglas-fir, white fir (*Abies concolor*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) in Colorado (Crockett and Hadow 1974). Madsen (1985) noted trembling aspen, which was uncommon on her study sites, to be important for nesting primary cavity-nesting birds. High use of trembling aspen by primary cavity-nesting birds was also observed by Bent (1939), Kilham (1971), and Erskine and McLaren (1972), Winternitz (1976, 1980), and Peterson and Gauthier (1985). British Columbia nest record cards at the B.C. Provincial Museum, for Yellow-bellied Sapsucker, Pileated Woodpecker, Hairy Woodpecker, Northern Flicker, and Downy Woodpecker indicated that deciduous trees, especially trembling aspen were used more frequently for nesting than conifers. Elsewhere, Pileated Woodpeckers were never reported to *prefer* trembling aspen, as in my study, but McClelland (1979) found them using black cottonwood and trembling aspen where these trees were large enough, and British Columbia nest records showed 15 of 41 Pileated Woodpecker nests to be in trembling aspen.

A number of other tree species were often preferred for nesting in different geographical areas. Bunnell and Allaye-Chan (1984) found that in forests dominated by western hemlock (*Tsuga heterophylla*), Douglas-fir, and western red cedar (*Thuja plicata*), western hemlock was preferred in a riparian area. In other sites, tree species were used in proportion to their availability. Their analyses were based on presence of old nest and roost cavities in dead trees. In forests consisting mainly of Douglas-fir, western larch, and ponderosa pine in north-central Washington, the latter 2 tree species were preferred for nesting (Madsen 1985). Preference for western larch over Douglas-fir was also observed in western Montana (McClelland 1977). Raphael and White (1984) found that most species preferred white fir over Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), and red fir (*Abies magnifica*) in the Sierra Nevada of northern California. In central Missouri, primary cavity-nesting birds preferred American sycamore (*Platanus occidentalis*) over a variety of tree species, mainly hardwoods, in an oak-hickory forest type (Brawn et al. 1984).

In my study area, Douglas-fir and other conifers were not used for nesting by primary cavity-nesting birds, although the density of dead conifers was comparable to those found in other studies. Avoidance of Douglas-fir for nesting has been noted by several other investigators (Crockett and Hadow 1975, McClelland and Frissell 1975, Bull and Meslow 1977, McClelland 1977, 1979, Madsen 1985). A list of tree species used by woodpeckers in the Pacific Northwest (Thomas 1979:381), partly based on original research and partly on literature survey, also showed little nesting use of Douglas-fir. Avoidance of Douglas-fir may be explained by its pattern of decay. Dead Douglas-fir deteriorate "from the outside in", i.e. decay softens the sapwood before it affects the heartwood (Wright and Harvey 1967, McClelland 1977, Cline et al. 1980). By the time the heartwood is sufficiently decayed for nest hole excavation, outer layers of wood are sloughing. In a western Oregon forest dominated by Douglas-fir with few dead trees of other species, Yellow-bellied Sapsucker, Pileated Woodpecker, Hairy Woodpecker, Red-breasted Nuthatch, and Northern Flicker nested mainly in Douglas-fir, using it in proportion to its availability (Mannan et al. 1980).

Differences in nest tree use among regions and forest types show that most primary cavity-nesting birds are flexible in their nesting use of tree species, and can adjust to local availability. It is evident, however, that some tree species tend to be preferred whenever they are available, whereas others are consistently avoided unless alternative species are scarce, although some site specific variation may occur. Desirability of a tree species for nesting seems to be determined mainly by its decay characteristics, as well as adequate size. Tree species preferences differ among species of primary cavity-nesters, probably because some are stronger excavators than others and because of differences in body size.

Surrounding vegetation

All nests of primary cavity-nesting birds in my study area were located in stands containing deciduous trees, which comprise only a small proportion of the whole study area. This strong selection may be explained by the preference for deciduous trees, which appear to be more suitable for nesting than the conifers in the study area. This explanation is supported by the fact that none of the conifers that occurred interspersed with the deciduous trees, contained nests. An additional reason for the preference for deciduous or mixed stands, which often grow in moister sites, may be characteristics of the stands themselves, such as high insect density and perhaps a more favourable microclimate, especially during the hot summers in the

Kamloops region.

Winternitz (1980) investigated possible causes for the strikingly high bird density, including cavity-nesters, in montane trembling aspen stands compared to surrounding Douglas-fir and ponderosa pine forest. She concluded that breeding bird density and species richness were related to surface water and ground moisture levels, presence of large and numerous insects in the understory, nest hole availability, *Fomes* infection, and edge effect. These findings support my hypothesis that trembling aspen stands are preferred over surrounding coniferous forest because of favourable stand characteristics as well as availability of trees preferred for nesting.

The influence of the vegetation, in the immediate vicinity of trees, on selection of nest trees has been demonstrated in a number of studies (Conner et al. 1975, Conner and Adkisson 1976, Raphael and White 1984, Hovis and Labisky 1985, Madsen 1985). I found this factor to have very little importance in nest tree selection. The reason is probably that my analyses were restricted to stands containing deciduous trees, because no nests were found in surrounding coniferous forests. Selection according to vegetation characteristics had therefore already taken place and vegetation differences within the deciduous stands may not have been important enough to further affect nest site selection or to outweigh the influence of tree characteristics on selection. Most of the characteristics describing the vegetation in the immediate vicinity of trees assessed structural features. My results thus suggest that tree species composition is a much better indicator of nesting habitat quality than structural features of the vegetation. The importance of tree species composition over vegetation structure in habitat selection by birds has also been stressed by Winternitz (1976) and Rice et al. (1984).

Breeding Densities

Breeding densities of primary cavity-nesting birds, calculated for the entire study area (Table 8), were low, compared to densities reported in other studies (Franzreb and Ohmart 1978, Mannan et al. 1980, Raphael and White 1984, Zarnowitz and Manuwal 1985). However, nesting was restricted to deciduous and mixed stands, which represented only a small portion of the study area. Breeding densities within these stands were much higher, but could not be calculated because of the patchy distribution of deciduous and mixed stands.

Nest Entrance Orientation

Primary cavity-nesting birds often appeared to prefer certain compass directions for placement of their nest entrances (Dennis 1971, Reller 1972, Conner 1975, Inoye 1976, Korol and Hutto 1984). Preferred directions varied among studies. These preferences have generally been attributed to climatic or thermal factors, i.e. primary cavity-nesting birds position their nest entrances in relation to directions of prevailing winds, or to optimize amount of incident solar radiation.

In my study, no compass direction was significantly preferred. This uniform orientation of entrance holes does not imply, that nest hole entrances were oriented randomly, or that entrance orientation is unimportant. Instead, the direction of the cavity entrances appeared to be chosen with respect to a combination of local factors, rather than in relation to overall climatic aspects. Cavities were observed to usually face away from obstructions, and downhill in nest trees on sloped ground. This placement provides easy access (Crockett and Hadow 1975) and perhaps facilitates early detection of approaching predators. In some cases, entrance orientation appeared to have been chosen with respect to features of the nest tree. I observed that entrance holes were sometimes situated beneath branch stubs or fungal conks, perhaps because decay was most advanced in those places (Conner et al. 1976), or because the projections provided shelter for the entrance hole. The frequent placement of nest holes

Table 8. Breeding densities[1] of primary cavity-nesting birds in the Orchard Lake and Skull Mountain Areas (2069 ha).

Bird species	Number[2] of pairs	Breeding density (pairs/100 ha)
Yellow-bellied Sapsucker	94	4.5
Pileated Woodpecker	6	0.3
Hairy Woodpecker	5	0.2
Red-breasted Nuthatch	12	0.6
Northern Flicker	9	0.4
Downy Woodpecker	3	0.1
Total	129	6.2

[1]conservative estimate, some nests may have been missed, especially of Red-breasted Nuthatch

[2]largest number of nests found during one breeding season

below branches has also been interpreted as a means of discouraging nest hole competitors (Short 1979), and may provide some protection from predators.

Influence of structural features of the nesting substrate was also noted by Korol and Hutto (1984). Conner (1975) argued that the slope of tree trunks was the most important factor in determining entrance orientation. Nest holes were most often placed on the underside of leaning trees, probably for protection from rain as well as from predators or competitors. There were too few leaning trees in my study to test this hypothesis. A variety of other local factors may influence orientation of nest entrances, the importance of each varying with tree location. I agree with Conner (1975) that apparent preferences for certain compass directions may often result from correlations with local factors, although in some cases compass direction itself may be important (Dennis 1971).

Comparison of Old Cavities and Active Nests

Active nests are generally considered to be a more accurate basis for analysing nest tree preferences than old, unoccupied cavities. Sources of error associated with using old cavities are that tree characteristics may have changed since an old cavity was built, and because old cavities cannot usually be located by the presence of woodchips, differences between dense and open stands in ease of detection may introduce a sampling bias. Furthermore, when old cavities are used, it is often difficult to determine which bird species excavated the cavity, or whether it was actually used as a nest, because old nest cavities may be confused with feeding holes or old, unfinished cavities. Analyses of nest tree selection in my study, however, were very similar, whether old, unoccupied cavities or active nests were used as a measure of nesting use. This similarity was mainly due to the fact that most of the 228 trees with old cavities also had active nests. Only 65 (28%) of the nest trees did not show any signs of previous nesting use (Table 9).

This high incidence of old cavities in active nest trees suggested that once a favourable nest tree had been found, it tended to be re-used in subsequent years. This behaviour of

Table 9. Number and percent of active nest trees with and without old cavities, and of nest trees found in 1984 that were re-used in 1985, apparently by the same species. Nests of unconfirmed species are excluded.

Bird species	Old cavities present	Old cavities absent	Nest trees found in 1984	1984 nest trees re-used in 1985
Yellow-bellied Sapsucker	124 (78)	35(22)	65	27(42)
Pileated Woodpecker	13 (65)	7(35)	10	1(10)
Hairy Woodpecker	2 (25)	6(75)	3	2(67)
Red-breasted Nuthatch	13 (54)	11(46)	12	2(17)
Northern Flicker	11 (65)	6(35)	9	2(22)
Downy Woodpecker	5(100)	-	2	-
all species	168 (72)	65(28)	101	34(34)

using the same nest tree for several seasons, excavating a fresh nest cavity each spring, seemed to be especially common for Yellow-bellied Sapsucker. Of the 65 Yellow-bellied Sapsucker nest trees found in 1984, 27 (42%) were re-used the following year. Frequent nest tree re-use by Yellow-bellied Sapsucker was also observed by Kilham (1971) and Erskine and McLaren (1972). Hairy Woodpecker showed an even higher percent of nest tree re-use, but this result is unreliable because of the small number of nests found for this species.

The similarity of results of nest tree selection analyses based on old and on active nests suggests, at least with respect to the tree and bird species in my study, that old cavities may be used in studies of nest tree selection to increase the sample size of nests. Survey of old cavities would be particularly useful when time constraints or scarcity of breeding birds make it difficult to find a sufficient number of active nests. Where nest tree re-use is uncommon, however, it may be better to rely only on active nests.

The one exception to the similarity between selection patterns based on old and on active cavities, was that active nests indicated a tendency to prefer trees with broken tops, whereas selection indices based on old cavities were negative for trees with broken tops. This discrepancy may be explained by the observation that dead nest trees tend to break at cavity height, a weak point along the trunk. Old cavities may therefore not be present on the remaining stump.

Primary cavity-nesting birds are generally thought to build new nest cavities each spring. I observed, however, that Yellow-bellied Sapsucker sometimes restricted its excavation efforts to building a new entrance into a previously used cavity. A possible advantage of this behaviour is reduced energy expenditure while still maintaining excavation activities which may be an important part of courtship rituals. Multiple entrances to a cavity may also provide escape routes and favourable nest trees can be re-used more often if the birds do not build a complete new cavity each year.

CHAPTER VI

MANAGEMENT IMPLICATIONS

Effects of Forest Management on Nesting Habitat of Primary Cavity-Nesting Birds

In the Orchard Lake and Skull Mountain Areas, which are dominated by Douglas-fir forest under uneven-aged management, primary cavity-nesting birds breed only in patches of deciduous or mixed forest. The tree species used for nesting are trembling aspen, paper birch, and thin-leaved mountain alder. Deciduous trees are, so far, not commercially harvested and most logging activity takes place outside the preferred nesting habitat. Some disturbance occurs when conifers are harvested from mixed stands, and because logging roads provide access to fuelwood cutters, who take mainly paper birch. However, a more important problem than the direct removal of potential nest trees, are longterm effects of forest management. Trembling aspen and paper birch are shade-intolerant seral species. Uneven-aged management and fire suppression tend to perpetuate coniferous climax vegetation, thereby creating adverse conditions for the regeneration of trembling aspen and paper birch, and thus impede continuous development of trees suitable for nesting.

Suggested Management Guidelines

Identification of trees preferred for nesting

Nest tree preferences of primary cavity-nesting birds in the Orchard Lake and Skull Mountain Areas are listed in Table 10. In trembling aspen and probably also in paper birch, presence of fungal conks is the best indicator of a tree's likelihood to be used for nesting. For a more accurate assessment of nest tree quality in trembling aspen, presence of scars, top condition, and tree diameter should be examined in conjunction with presence of conks. Tree condition and height did not appear to be reliable indicators of nest tree quality in trembling aspen, at least for, Yellow-bellied Sapsucker, whose large nest sample dominated

Table 10. Attributes of trees preferred for nesting by primary cavity-nesting birds in the Orchard Lake and Skull Mountain Areas. An asterisk indicates that no significant preference was detected. Mean values (Table 2) should be used for nest tree diameter where no significant preference was observed.

Variable	Stronger excavators[1]	Weaker excavators[2]
Tree species	Trembling aspen	Trembling aspen or paper birch
Tree diameter (cm dbh)	S: ≥30 P: ≥40 H: *	N: * F: * D: *
Tree condition	*	dead or dead top
Fungal conks	present	present
Scars	S: present P: * H: *	N: * F: * D: *
Top condition[3]	*	broken

[1]Yellow-bellied Sapsucker(S), Pileated Woodpecker (P), and Hairy Woodpecker (H)
[2]Red-breasted Nuthatch (N), Northern Flicker (F), and Downy Woodpecker (D)
[3]inlcudes all tree conditions

analyses. Primary cavity-nesting birds did not nest in live parts of paper birch. Tree condition therefore is a valuable indicator of nest tree quality in this tree species. Old cavities, especially if numerous, also identify preferred nest trees.

It is often difficult to assess differences in habitat quality, in terms of their influence on an animal's fitness, because decline in survival and reproductive success due to suboptimal habitat conditions, may be a gradual, longterm process, or because differences in habitat quality may only become apparent during low frequency, stochastic events such as weather extremes. It is much easier and more effective to evaluate habitat quality by observing how the animal responds to its habitat, and to manage for its preferences, because these preferences are the result of evolutionary processes and are thus likely to represent adaptive behaviour that maximizes the animal's fitness within the framework of local availability of habitat components. Similar reasoning was employed by Conner (1979), when he suggested that management guidelines should be based on mean rather than minimum nest tree dimensions. However, mean tree size used is affected by availability of tree sizes in the forest and may not necessarily represent a preference. Preferred nest tree dimensions, if such preferences are detected, should thus be used in managing for cavity-nesters. Knowing nest tree preferences allows enhancement of nest habitat quality, i.e. increasing the availability of *preferred* trees in the forest may result in higher population densities of primary cavity-nesters than can be achieved by providing equal numbers of trees that may be usable but are of lower quality. Some problems associated with evaluating preference have been pointed out, especially regarding realistic assessment of availability (Neu et al. 1974, Cock 1978, Johnson 1980, Lechowicz 1982).

Every effort should be made to retain trees with characteristics preferred for nesting. Trees of lower quality should also be retained, where not enough trees with preferred characteristics are available to obtain the number of trees required to support a particular population density of primary cavity-nesters. The number of trees required has often been calculated using the formula:

$$(Y) = (A) \times (B) \times (C)$$

where (A) = maximum population density, (B) = number of trees used annually for nesting and roosting by each pair, (C) = buffer of trees, because not all apparently suitable trees will be used (Thomas et al. 1976, Thomas 1979:68–69, Raphael and White 1984). Potential nest trees must be adequately spaced to account for the birds' territorial requirements.

Only primary cavity-nesting birds were examined in this study. It is assumed that managing for primary cavity-nesting birds will ensure a continuous supply of nest holes for secondary cavity-nesters (Bull 1978, Mannan et al. 1980).

Depending on their availability, different tree species are used for nesting by primary cavity-nesting birds in different areas. Characteristics of preferred nest trees (size, tree condition, pattern of decay) can vary among tree species, and tree species differ in their ecology and in the role they play in forest management. Nest tree preferences and management guidelines can therefore not be generalized among studies involving different tree species. Some tree species tend to be preferred whenever they are available and others are consistently avoided, although some site-specific variation may occur. This ranking of tree species can be used to predict which of the available tree species is most important for nesting in areas that have not been studied, as long as the species composition of trees and primary cavity-nesting birds is known. Nest tree preferences and management implications specific to the preferred tree species can then be extracted from the literature. More studies are needed to identify patterns of nest tree selection for every tree species, and to test the consistency of tree species-specific preferences among different sites and regions.

Ensuring continuous development of trees preferred for nesting

Presently, the tree species used for nesting in the study area (Trembling aspen, paper birch) occur mainly as maturing or overmature serals (as defined by Walmsley et al. 1980:64). These seral stages are most valuable as nesting habitat for primary cavity-nesters, because trees are large enough and decay is far enough advanced, providing an abundance of trees with characteristics preferred for nesting. As succession proceeds, these seral stages are replaced by a climax vegetation of hybrid spruce, and in some sites, Douglas-fir, which are not used for nesting.

The goal in managing for cavity-nesters is, therefore, to ensure the continuous availability of maturing and overmature seral stages. This can be achieved by creating a mosaic of successional stages, by periodically creating openings in sites suitable for the regeneration of trembling aspen and paper birch, so that at any point in time, some stands are at the stages most valuable as nesting habitat.

Factors that may influence successful regeneration of deciduous trees in these openings (e.g. size of clearing, site treatment, grazing pressure) need to be examined and managed accordingly. Not all trembling aspen and paper birch will develop into nest trees of high quality. Especially the large trees preferred by Pileated Woodpecker do not develop on every site. It would therefore be useful to examine how site conditions influence the development of trees preferred for nesting. Timing of this patchy stand rejuvenation is important to ensure continuous availability of maturing and overmature seral stages. At what intervals openings should be created, depends on the rate of forest succession, timing of incidence and spread of decay (when do trees become usable for nesting?, how long are they usable?), and on features of each tree species' reproductive biology. The number of old cavities may be used to estimate how many years trees remain usable for nesting. However, difficulty of distinguishing unfinished old cavities from old nests, and loss of conspicuousness of cavity entrances in live trees due to healing, reduce the reliability of such estimates.

Recommendations outlined so far pertain only to situations where trembling aspen and paper birch are not commercially cut. In areas where these tree species are harvested, or eliminated to reduce competition with conifers, integration of forestry and habitat for cavity-nesters is much more difficult, because trembling aspen and paper birch are cut before they are large and decayed enough to serve as nest trees. To maintain habitat for cavity-nesters, development of maturing and overmature deciduous seral stages should be allowed in some stands.

Foraging habitat

My study examined only preferences related to nesting. A positive relationship between density of suitable nest trees and density of cavity-nesters is well documented (Haapanen 1965, Conner et al. 1975, McClelland and Frissell 1975, Bull and Meslow 1977, Scott 1979, Dickson et al. 1983, Scott and Oldemeyer 1983, Raphael and White 1984, Madsen 1985, Zarnowitz and Manuwal 1985), and suggests that availability of suitable nest trees often limits population sizes of cavity-nesters. However, it is also important to recognize habitat needs related to foraging, and to consider them in forest management plans. Primary cavity-nesting birds forage on a variety of woody substrates, such as standing live or dead trees, stumps, down logs, and woody debris. Some species, especially Northern Flicker, also forage on the ground, and I observed Yellow-bellied Sapsucker and Red-breasted Nuthatch catching insects in flight. Standing dead or decaying trees may be the most important feeding substrate for resident primary cavity-nesters after snowfall.

Although conifers were not used for nesting in my study area, signs of wood excavation or bark scaling by foraging primary cavity-nesters were very prevalent on dead conifers, in mixed deciduous stands as well as in coniferous forest. Of the dead conifers, 72% showed feeding signs, whereas only 38% of dead deciduous trees had been used for feeding. Almost none of the live conifers showed evidence of foraging. The great variability in density of dead conifers, mainly due to changing wildlife tree management policies, and the patchy distribution of deciduous trees, prevented meaningful comparisons of the relative availability of dead deciduous and coniferous trees, so that preferences could not be evaluated. The prevalence of feeding signs on dead conifers, however, strongly suggested their importance as foraging substrates for primary cavity-nesting birds. Raphael and White (1984) and Madsen (1985) found that foraging primary cavity-nesting birds preferred large trees. A continuous supply of large dead conifers should be ensured by retaining selected trees of different ages and managing some stands on an extended rotation basis, which would also benefit other wildlife species that require an old growth component.

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