

# Roost-site Preferences of Big Brown Bats (*Eptesicus fuscus*) and Silver-haired Bats (*Lasionycteris noctivagans*) in the Pend d'Oreille Valley in Southern British Columbia

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## ABSTRACT

I examined the roost-site preferences of big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) in the Pend d'Oreille River Valley (POV) in southern British Columbia during the summer of 1995. Roost trees were located via radio-telemetry, then observed at dusk to confirm use and determine colony sizes. I found a total of 27 roost trees used by the two species. Both big brown bats and silver-haired bats preferred large trees (either tall or with a large DBH) that were uncluttered by surrounding trees relative to available trees in the immediate vicinity of the roost, and in other areas of the same stand. Both species preferred trembling aspen. Big brown bats preferred trees in decay stages two and six, whereas silver-haired bats exhibited no decay-stage preferences. When the tree and site characteristics of roost trees used by big brown bats and silver-haired bats were compared, only the height of the tree relative to canopy height discriminated between them. Big brown bats prefer trees that are higher relative to the canopy than silver-haired bats. This information was used to develop a set of management recommendations for maintaining bat roosting habitat in the POV.

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## INTRODUCTION

The POV occurs in the Southern Interior Mountains Ecoprovince in southern British Columbia, just north of the U.S. border. The valley is unique because it has an east-west orientation, which results in an abundance of south-facing slopes and associated dry, warm climate. Forests in the POV have been modified both by conventional logging practices and hydroelectric developments, including dams and associated power lines. Surveys for bats in the POV have found that the valley contains large numbers of at least 10 species (Rasheed and Holroyd 1995; Vonhof 1995a, b). Of particular interest was the extremely high abundance of relatively large bat species, such as big brown bats (*Eptesicus fuscus*) and silver-

haired bats (*Lasionycteris noctivagans*), which can be difficult to capture and are caught in low numbers in other regions of British Columbia (M. Vonhof, pers. obs.; Rasheed and Holroyd 1995).

The apparent abundance of bats in the POV provided an excellent opportunity to examine the roosting requirements of forest-dwelling bats. In summer, bats spend over half of each day in a roost site, and because of this, roosts play a vital role in the lives of bats. Roosts may provide bats with a thermally stable environment or space in which they receive protection from the elements (Vaughan 1987), and in which individuals can cluster together, thereby reducing the energetic costs of thermoregulation (Trune and Slobodchikoff 1976; Kurta 1985). Roosts may also provide protection from predators (Fenton 1983; Tidemann and Flavel 1987), and serve as sites for social interactions with conspecifics (Morrison 1980). The choices made by bats with respect to the type and location of roost sites likely have a strong influence on their survival and fitness.

Much of the detailed work on the roosting ecology of bats has centred on bats roosting in caves or man-made structures, as these locations are often relatively accessible to humans and easy to find (see Kunz 1982). In contrast, few studies have examined the ecology of bats roosting in trees. Most records of tree-roost sites are simply descriptions or anecdotes of single colonies in trees (e.g., Barclay and Cash 1985; Parsons et al. 1986; Kurta et al. 1993a, b; see references in Kunz 1982). A few studies have examined specific tree characteristics and compared them to random samples of available trees to gain some indication of site-selection by bats (e.g., Barclay et al. 1988; Taylor and Savva 1988; Lunney et al. 1988). However, these studies only examined small numbers of characteristics and could not provide a complete picture of the specific tree or site characteristics selected by bats.

Recently, Vonhof and Barclay (in press) provided an in-depth look at the roosting requirements of forest-dwelling bats. Out of 22 tree and site characteristics that they measured, only three significantly discriminated between roost and available trees: tree height, distance to the nearest available wildlife tree, and percentage of canopy closure. Bats preferred tall trees close to other wildlife trees situated in areas with open canopies. Furthermore, bats preferred western white pine trees, and to a lesser extent, ponderosa pine trees, in intermediate stages of decay. The results provided testable predictions for the roost-site preferences of bats, and further studies in other areas with different forest types may determine the generality of their results.

This paper summarizes the results of a study to investigate the roost-site preferences of forest-dwelling bats in the POV. Reproductive female *Eptesicus fuscus* and *Lasionycteris noctivagans* were outfitted with radio-transmitters in order to locate roost sites. The tree and site characteristics of the roost trees used by the two species could then be compared to each other, as well as to randomly selected trees, to determine which characteristics bats select. This information was then used to develop management recommendations for the maintenance of bat-roosting habitat in the POV.

Roost sites were located using radio-telemetry. Bats were captured in mist nets set across marshes, small ponds, edges of a dam reservoir, clearcut edges, and across roads at various locations and elevations throughout the valley. Captured bats were identified to species, sexed, and aged as adults or juveniles (young of the year) based on the degree of ossification of the metacarpal-phalange joints (Racey 1974). I measured mass and forearm length and assessed reproductive condition (Racey 1974) for all captured individuals.

I attached small (0.53–0.73 g; Model BD2, Holohil Systems Ltd., Woodlawn, Ontario) radio-transmitters to pregnant or lactating female *Eptesicus fuscus* ( $n = 8$ ) and *Lasionycteris noctivagans* ( $n = 10$ ). Transmitters were attached between the scapulae of individual bats using Skin-Bond® (Canadian Howmedica, Guelph, Ontario) surgical adhesive. I located roost sites during the day by tracking radio signals with at least two receivers (Lotek STR 1000, Lotek Engineering Inc., Newmarket, Ontario) and two- or three-element Yagi antennae. All but three of the roosts found by radio-telemetry were verified by watching the tree at dusk for emerging bats.

Once roosting sites had been located, I measured a range of tree characteristics for all roosts (Appendix 1). I measured diameter at breast height (DBH), and determined all tree heights, entrance heights, and slopes with a clinometer and entrance aspect with a compass corrected to true north. Two observers independently estimated the percentage of bark remaining on the tree, and the mean was taken. In addition, I measured the horizontal distance to and height of the nearest tree of the same or greater height, which is defined as the closest tree to the roost in a 90° arc extending out from the roost entrance.

I classified each roost tree into one of nine decay stages, based on the British Columbia Wildlife Tree Classification System (Backhouse and Lousier 1991; Vonhof 1995a), which takes into account characteristics of the tree, such as the percentage of bark remaining, number of limbs present, condition of the top, and condition of the heartwood and sapwood. I only measured trees falling into decay stages two to seven, as by definition decay-stage one trees and decay-stage eight to nine trees provide no suitable roosting opportunities for bats.

I established a 17.8 m radius (0.1 ha) plot around each roost tree, and within it measured two randomly selected available trees, defined as trees in decay stages two to seven not known to contain bats. If the plot contained less than two available trees, the closest available trees outside the plot were measured. I also measured site characteristics within the plot. The percentage of canopy closure within the plot was visually estimated by at least two observers and the mean was taken. I measured the height of at least two trees (range two to five) within the canopy using a clinometer, and took the mean to estimate canopy height within the plot.

I also established two plots located in other areas of the same stand. I located plots by selecting a random point between 100 and 300 m from the roost tree along each of two transects established in randomly selected directions that differed by greater than 90°, and determined the nearest available tree to the random point (focal tree). If this random point lay

outside the stand, I chose another random direction and distance, and located the nearest available tree. I established a 17.8 m radius (0.1 ha) plot around the focal tree and measured the tree characteristics of the focal tree in the same fashion as for roost trees, and measured the site characteristics of the plot.

I performed a series of stepwise discriminant function analyses, including the variables outlined in Appendix 1, to determine whether the tree and site characteristics of roost trees used by the various bat species differed, and to determine which tree and site characteristics the bat species select relative to available trees. All roost trees were considered together in all comparisons of roost trees regardless of the reproductive condition of the bats, because sample sizes did not permit separate analyses for pregnant and lactating bats. In all cases I then applied a canonical discriminant function analysis to the same data with the significant variables from the stepwise analysis to determine the placement of these variables along the discriminant function. This analysis provided the total sample standardized canonical coefficients ( $TSSCC$ ) for each variable, and classification error rates based on cross-validation. The relative magnitude of the  $TSSCC$  is a measure of the contribution of each variable to the discrimination, and its sign indicates to which group individual trees belong as their value for the particular variable increases. Separate analyses were performed between roost trees and available trees from two geographic scales: available trees from the immediate vicinity of the roost tree (within the 0.1 ha circular plot around each roost tree), and available trees from other areas of the same stand. Because tree species and decay stage are categorical and could not be included in the discriminant function analyses, I analyzed them separately using randomization tests, comparing the roost trees used by *E. fuscus* and *L. noctivagans*, and comparing roost trees with available trees.

## RESULTS

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I found a total of 27 roost trees using radio-telemetry. Fifteen roosts were used by *E. fuscus*, and 12 by *L. noctivagans*. *Eptesicus fuscus* roosted in natural hollows and abandoned primary cavity excavator (PCE) hollows in almost equal numbers ( $n = 5$  and 6, respectively), and in one instance also roosted in a crack caused by a lightning strike. I could not identify the nature of the roost for three of the roosts used by *E. fuscus*. *Lasionycteris noctivagans* tended to roost more often in abandoned PCE hollows ( $n = 8$ ) than natural hollows ( $n = 4$ ), but did not roost in cracks. Colony sizes varied widely both within and between the two bat species, but *E. fuscus* colonies (mean: 34; range: 2–61) were significantly larger than *L. noctivagans* (mean: 12; range: 1–35) colonies (ANOVA:  $F_{1,24} = 13.54$ ,  $P < 0.01$ ). Colony size was not significantly correlated with either tree height or DBH for either *E. fuscus* or *L. noctivagans* ( $P > 0.05$  in all cases).

### *Eptesicus fuscus* Roost- Tree Preferences

Of the 19 variables initially entered into the stepwise discriminant function analysis, only two significantly discriminated between *E. fuscus* roost trees and available trees in the immediate vicinity of the roost tree (Table 1).

TABLE 1 Summary of the stepwise discriminant function analysis on tree and site characteristics, comparing roost trees used by *E. fuscus* with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. The centroids for roost trees and available trees lie at the positive and negative ends of the discriminant axis, respectively.

Variable	Order included	Partial			
		<i>F</i>	<i>P</i>	<i>R</i> <sup>2</sup>	TSSCC
<i>Immediate vicinity</i>					
Horizontal distance to nearest tree of same or greater height	1	17.84	0.0001	0.29	0.75
DBH	2	4.93	0.0318	0.11	0.67
<i>Stand</i>					
Tree height	1	25.12	0.0001	0.40	1.32
Number limbs remaining	2	9.19	0.0045	0.20	-0.71
Percent bark remaining	3	8.64	0.0058	0.20	0.70
DBH	4	5.94	0.0202	0.15	0.53

The horizontal distance to the nearest tree of the same or greater height accounted for 29% of the variation between roost and available trees, and DBH accounted for 11%. Based on the canonical discriminant function analysis, in this and subsequent analyses, the centroid for roost trees was at the positive end of the discriminant axis, and the centroid for available trees was at the negative end. The TSSCC's for both horizontal distance to the nearest tree of the same or greater height and DBH were positive, indicating that roost trees tend to be further away from other tall trees and have a greater DBH than available trees from the immediate vicinity of the roost. The classification error rates for roost trees was relatively high (53%), whereas that for available trees was relatively low (13%). The overall classification error rate was 33%.

Four variables significantly discriminated between *E. fuscus* roost trees and available trees from other areas of the same stand: tree height, number of limbs remaining, percentage of bark remaining, and DBH (Table 1). Tree height was by far the strongest discriminating variable, explaining 40% of the variation between roost and available trees. The other three variables each explained between 15–20% of the total variation. Overall, the combination of the four discriminating variables explained 95% of the variation between *E. fuscus* roost and available trees from other areas of the same stand. Based on the canonical discriminant function analysis, the centroid for *E. fuscus* roost trees was at the positive end of the discriminant axis and the centroid for available trees was at the negative end. The TSSCC's for tree height, percentage of bark remaining, and DBH were positive, indicating that *E. fuscus* roost trees tend to be taller, have a greater diameter, and have more bark remaining than available trees from other areas of the same stand. In contrast, the TSSCC for number of limbs remaining was negative, suggesting that *E. fuscus* roost trees have fewer limbs than do available trees from other areas of the same stand. The classification error rates for roost and available trees were low (0% and 7%, respectively), with an overall error classification rate of 4%.

TABLE 2 Summary of correlations between significant discriminating variables, and between significant discriminating variables and other variables included in the discriminant function analysis comparing roost trees used by *E. fuscus* with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. Values listed in the table are correlation coefficients ( $r$ ). Blank spaces indicate no significant correlation.

Variable	Variable	Immediate vicinity	Other areas of same stand
Tree height	DBH	0.64***	0.61***
Tree height	Horizontal distance to tree of $\geq$ height	0.57***	0.55***
DBH	Horizontal distance to tree of $\geq$ height	0.55***	
DBH	Height of tree of $\geq$ height	0.35*	
DBH	Tree height relative to canopy height	0.65***	
DBH	Horizontal distance to nearest available tree		0.37*
Horizontal distance to tree of $\geq$ height	Tree height relative to canopy height	0.51***	
Horizontal distance to tree of $\geq$ height	Horizontal distance to nearest available tree	0.30*	
Horizontal distance to tree of $\geq$ height	Horizontal distance to nearest neighbour tree	0.53***	

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

I found significant positive correlations between the significant discriminating variables and other measures of tree size and clutter around the roost tree when comparing *E. fuscus* roost trees with both available trees from the immediate vicinity of the roost and available trees from other areas of the same stand (Table 2).

*Eptesicus fuscus* did not roost at random with respect to the availability of different tree species when compared to either available trees from the immediate vicinity of the roost tree (randomization test;  $G = 34.79$ ,  $P < 0.001$ ; Figure 1) or to available trees from other areas of the same stand ( $G = 34.87$ ,  $P < 0.001$ ; Figure 1). *E. fuscus* preferred trembling aspen (*Populus tremuloides*), and to a lesser extent ponderosa pine (*Pinus ponderosa*). *E. fuscus* roosted less frequently than expected in Douglas-fir (*Pseudotsuga menziesii*), and did not roost at all in any of the other five available tree species. All five natural-cavity roosts and six abandoned PCE hollow roosts were located in trembling aspen. The only crack roost used by *E. fuscus* was located in a ponderosa pine tree. Two of the three roosts for which I could not determine the nature of the cavity were located in trembling aspen, and the third was in a Douglas-fir tree.

*Eptesicus fuscus* also did not roost at random with respect to the availability of different decay stages when compared to available trees from the immediate vicinity of the roost tree (randomization test;  $G = 26.45$ ,  $P < 0.001$ ; Figure 2) or to available trees from other areas of the same stand ( $G = 21.63$ ,  $P < 0.001$ ; Figure 2). *E. fuscus* roosted in trees of decay stages two, three, five, and six, and roosted more frequently than expected in decay-stage two trees, based on their availability in the immediate vicinity of the roost tree and in other areas of the same stand. *E. fuscus* roosted more frequently in decay-stage six trees based on their availability in the immediate vicinity of the roost tree only. Three natural-cavity roosts were found in trees in decay-stage two, and the other two were found in trees in decay stages five and six. Roosts in abandoned PCE

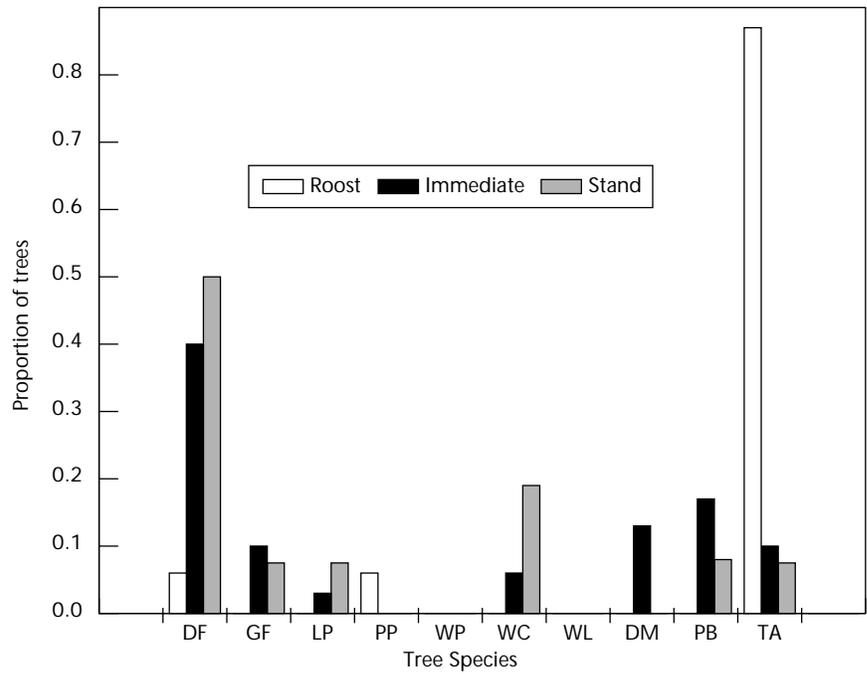


FIGURE 1 The proportion of *E. fuscus* roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in the 10 major tree species found in the POV. Tree species notation is as follows: DF = Douglas-fir, GF = grand fir, LP = lodgepole pine, PP = ponderosa pine, WP = western white pine, WC = western redcedar, WL = western larch, DM = Douglas maple, PB = paper birch, TA = trembling aspen.

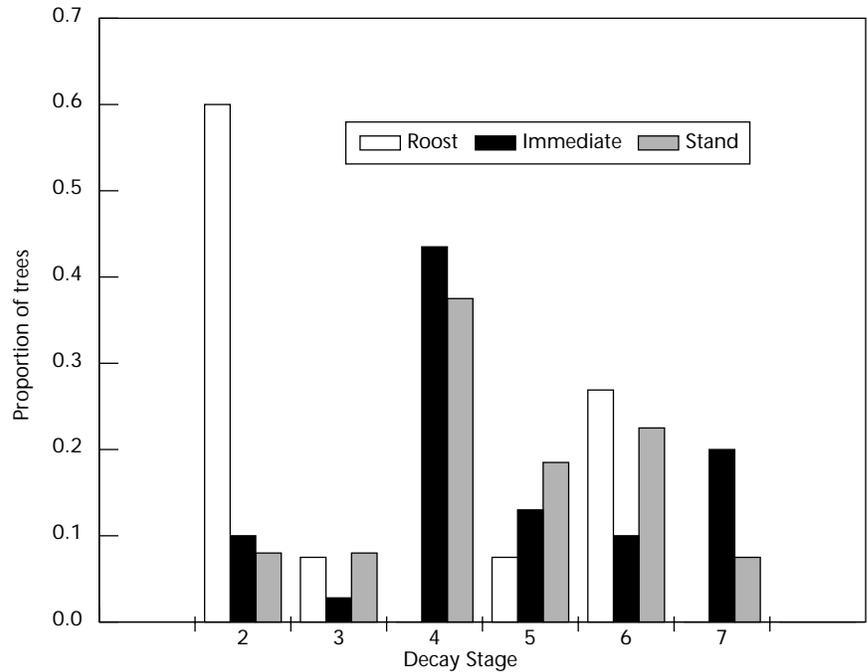


FIGURE 2 The proportion of *E. fuscus* roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in each of the six decay stages.

hollows were found most often in decay-stage two trees ( $n = 4$ ), but were also found in decay-stage six trees ( $n = 2$ ). The single crack roost was on a decay-stage two tree.

Three of the 19 variables that initially entered into the stepwise discriminant function analysis significantly discriminated between *L. noctivagans* roost trees and available trees in the immediate vicinity of the roost tree (Table 3). The horizontal distance to the nearest tree of the same or greater height, the horizontal distance to the nearest neighbouring tree, and tree height all accounted for approximately 17–20% of the variation between roost and available trees. The TSSCCs for both horizontal distance to the nearest tree of the same or greater height and tree height were positive, indicating that roost trees tend to be further away from other tall trees and be taller than available trees in the immediate vicinity of the roost. The TSSCC for horizontal distance to the nearest neighbouring tree was negative, suggesting that roost trees tend to be closer to neighbouring trees than available trees. Based on the magnitude of the TSSCCs, horizontal distance to the nearest tree of the same or greater height was the strongest discriminating variable, followed by horizontal distance to the nearest neighbouring tree, and then tree height. The classification error rates for roost and available trees were 33% and 17%, respectively, with an overall error rate of 25%.

Only one variable (DBH) significantly discriminated between *L. noctivagans*' roost trees and available trees from other areas of the same stand, and it explained over 35% of the variation between roost and available trees (Table 3). The TSSCC for DBH was large and positive, indicating that *L. noctivagans*' roost trees tend to have greater diameters than available trees from other areas of the same stand. The classification error rates for roost and available trees were relatively high (25% and 29%, respectively), with an overall error classification rate of 27%.

When comparing *L. noctivagans*' roost trees with both available trees from the immediate vicinity of the roost and available trees from other

TABLE 3 Summary of the stepwise discriminant function analysis on tree and site characteristics, comparing roost trees used by *L. noctivagans* with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. The centroids for roost trees and available trees lie at the positive and negative ends of the discriminant axis, respectively.

Variable	Order included	Partial			
		F	P	R <sup>2</sup>	TSSCC
<i>Immediate vicinity</i>					
Horizontal distance to nearest tree of same or greater height	1	6.79	0.0135	0.17	1.02
Horizontal distance to nearest neighbouring tree	2	8.06	0.0077	0.20	-0.84
Tree height	3	7.35	0.0107	0.19	0.70
<i>Stand</i>					
DBH	1	17.80	0.0002	0.36	1.20

TABLE 4 Summary of correlations between significant discriminating variables, and between significant discriminating variables and other variables included in the discriminant function analysis comparing roost trees used by *L. noctivagans* with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. Values listed in the table are correlation coefficients ( $r$ ). Blank spaces indicate no significant correlation.

Variable	Variable	Immediate vicinity	Other areas of same stand
Tree height	DBH	0.39*	0.43**
DBH	Horizontal distance to tree of same or greater height	0.35*	0.35*
DBH	Height of tree of same or greater height		0.38*

\*  $P < 0.05$ , \*\*  $P < 0.01$

areas of the same stand, I found significant positive correlations between the significant discriminating variables and other measures of tree size and clutter around the roost tree (Table 4).

*L. noctivagans* did not roost at random with respect to the availability of different tree species when compared to available trees from other areas of the same stand (randomization test;  $G = 19.54$ ,  $P < 0.01$ ; Figure 3), but did when compared to available trees from the immediate vicinity of the roost tree ( $G = 12.22$ ,  $P > 0.05$ ; Figure 3), although there was a trend

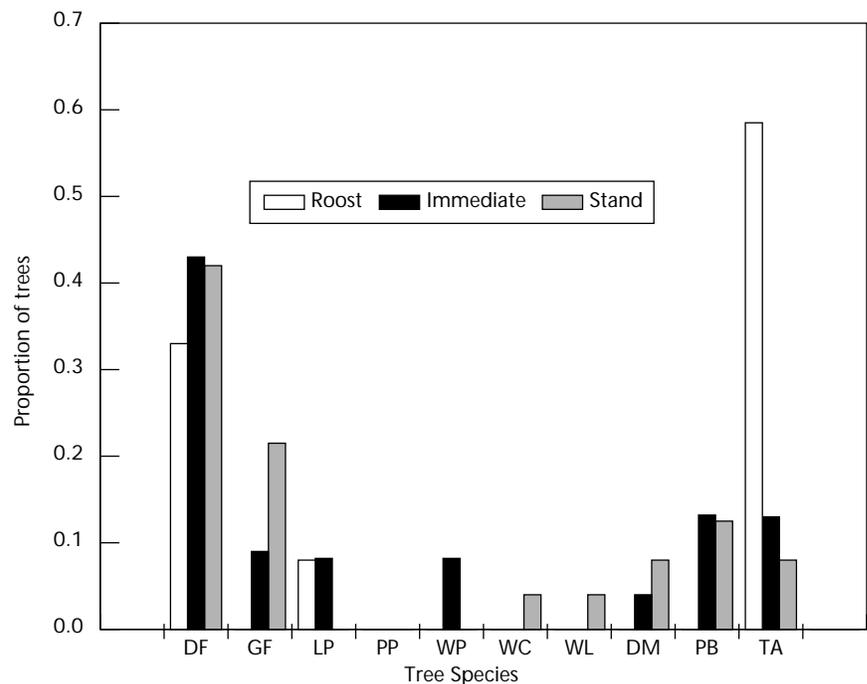


FIGURE 3 The proportion of *L. noctivagans* roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in the 10 major tree species found in the POV. Tree species notation is as in Figure 1.

towards preferring particular tree species. Relative to available trees from other areas of the same stand, *L. noctivagans* preferred trembling aspen and lodgepole pine (*Pinus contorta*). *L. noctivagans* used Douglas-fir slightly less frequently than expected, based on its availability in other areas of the same stand. *L. noctivagans* did not roost in any of the other six available tree species. Four of the eight roosts in abandoned PCE hollows were located in Douglas-fir, three in trembling aspen, and one in lodgepole pine. All four natural-cavity roosts were in trembling aspen.

*L. noctivagans* roosted at random with respect to the availability of different decay stages, whether I considered available trees from the immediate vicinity of the roost (randomization test;  $G = 7.53$ ,  $P > 0.25$ ; Figure 4) or available trees from other areas of the same stand ( $G = 8.15$ ,  $P > 0.10$ ; Figure 4). Roosts in abandoned PCE hollows used by *L. noctivagans* were found in all decay stages except for decay-stage three. Three of the four natural-cavity roosts were found in decay-stage two trees, and the other was found in a decay-stage five tree.

Comparing *Eptesicus fuscus* and *Lasionycteris noctivagans* Roost-Tree Preferences

Only one variable significantly discriminated between roost trees used by *E. fuscus* and *L. noctivagans*: tree height relative to canopy height ( $F = 17.84$ ,  $P < 0.001$ ). This variable explained a relatively low proportion (partial  $R^2 = 29\%$ ) of the variation between the two groups of roost trees. Based on the canonical discriminant function analysis, the centroid for *E. fuscus* roost trees was at the positive end of the discriminant axis and the centroid for *L. noctivagans* roost trees was at the negative end. The TSSCC for tree height relative to canopy height (0.75) was positive, indicating that *L. noctivagans* roost trees tended to be further beneath the

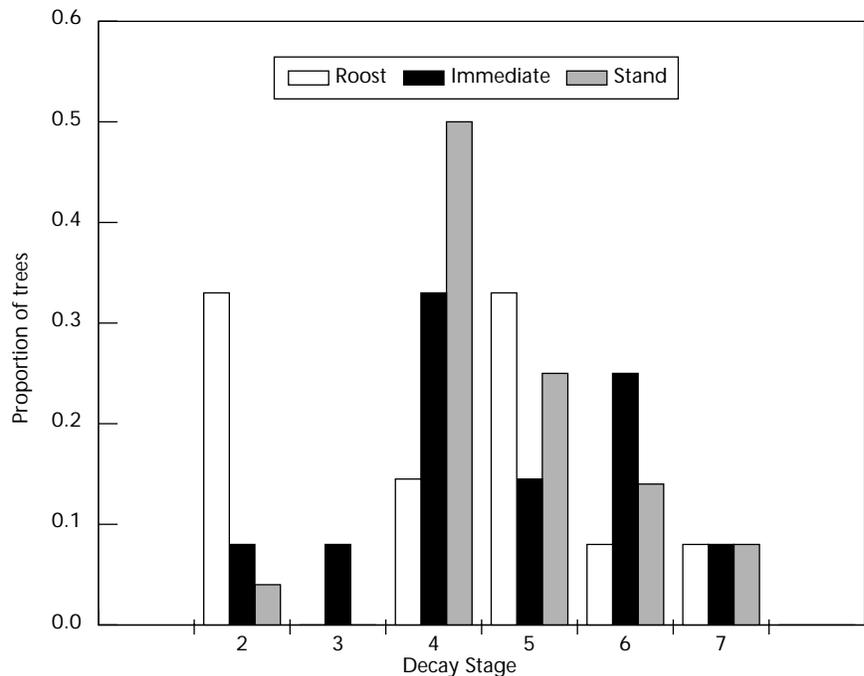


FIGURE 4 The proportion of *L. noctivagans* roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in each of the six decay stages.

canopy than *E. fuscus* roost trees. The classification error rates for *E. fuscus* roost trees and *L. noctivagans* roost trees were 27% and 33%, respectively, with an overall error classification rate of 30%.

I found significant positive correlations between tree height relative to canopy height and DBH, and tree height relative to canopy height and tree height, and negative correlations between tree height relative to canopy height and slope, and tree height relative to canopy height and canopy height (Table 5).

I found no significant difference between the species of tree roosts used by *E. fuscus* and *L. noctivagans* (randomization test;  $G = 6.19$ ,  $P > 0.05$ ). However, I did find a significant difference between the decay stages used by the two bat species ( $G = 11.04$ ,  $P < 0.05$ ). *E. fuscus* used decay-stage two and six trees more often than *L. noctivagans*, and, conversely, *L. noctivagans* used decay-stage four and five trees more often than did *E. fuscus*.

TABLE 5 Summary of correlations between the significant discriminating variable and other variables included in the discriminant function analysis comparing roost trees used by *E. fuscus* and *L. noctivagans*.

Variable	Variable	<i>r</i>
Tree height relative to canopy height	DBH	0.56**
Tree height relative to canopy height	Tree height	0.93***
Tree height relative to canopy height	Slope	-0.40*
Tree height relative to canopy height	Canopy height	-0.51**

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

## DISCUSSION

In general, both big brown bats and silver-haired bats preferred either large-diameter or tall trees that were relatively far away from surrounding trees. Similarly, Vonhof and Barclay (in press) found that bats prefer tall trees close to other available trees that are surrounded by an open canopy, while other studies on tree-roosting bats have shown that bats prefer large-diameter trees (e.g., Barclay et al. 1988; Lunney et al. 1988; Taylor and Savva 1988; Brigham 1991) rather than tall trees. Similarly, in some studies, cavity-nesting birds (Harestad and Keisker 1989; Lundquist and Mariani 1991) prefer large-diameter snags, whereas in other studies a preference for tall trees has been observed (Nilsson 1984; Raphael and White 1984; Rendell and Robertson 1989). In all analyses comparing roost trees with available trees I found that either tree height or DBH, or both, significantly discriminated between the two groups of trees. I also found that tree height and DBH were significantly positively correlated, such that the tree height variable in the discriminant function analysis also included information with respect to DBH, and vice versa. Thus, tree size may be the more appropriate factor selected by bats, rather than any particular measure of tree size. The two measures of tree size also contain information with respect to clutter around the roost tree. Tree height and DBH were generally positively correlated with the measures of clutter around

the roost tree that significantly discriminated between roost and available trees (i.e., horizontal distance to the nearest tree of the same or greater height, and horizontal distance to the nearest neighbouring tree), such that large trees are relatively uncluttered. Therefore, to receive the potential benefits of uncluttered trees, bats need only select large trees, or vice versa.

Bats may select large, uncluttered trees for several reasons. The diameter of a tree may set an upper limit to the size of the colony of bats that can form in a particular cavity. This may be especially important for reproductive females, as colonial bats may experience significant thermal and energetic benefits by clustering (Trune and Slobodchikoff 1976; Kurta 1985). Colony sizes, particularly for big brown bats, were generally large (up to 61 individuals), and small trees would simply not be able to support large colonies of bats. The potential size of cavities would be extremely important around the time of parturition, as the number of individual bats using the same space increases dramatically when females begin to give birth. Clutch size within cavity-nesting bird species increases with increasing cavity size (e.g., Rendell and Robertson 1989), and the size of the cavity may limit the size of maternity colonies of bats in tree roosts. In addition, the larger a tree is at the time of death the longer it will stand (Cline et al. 1980; Newton 1994), and the greater the time it will potentially remain as a useful roost site to bats.

Bats may also gain significant energetic benefits by choosing trees that are exposed to sunlight. Low roost temperatures slow fetal and juvenile development in bats (Racey 1973; Tuttle 1976; Racey and Swift 1981), and seasonal low temperatures reduce the number of reproductive females and the number of young successfully fledged (Grindal et al. 1992; Lewis 1993). Thus, reproductive female bats may benefit energetically by selecting roosts that are heated by the sun for at least part of the day. Tall trees relatively uncluttered by surrounding trees are exposed to sunlight for a greater length of time than are trees with canopy cover. Indeed, nearly all of the roost trees that I found, including all of the maternity colonies, were exposed to direct sunlight for at least part of the day. Although neither big brown bats nor silver-haired bats preferred trees with a particular orientation, a cavity in the centre of a tree exposed to sunlight will be heated via conduction through the walls of the cavity, no matter which side of the tree is exposed to the sunlight (Vonhof and Barclay in press).

Flight is costly (Speakman and Racey 1991), and a clear flight path in front of the roost entrance on a large, uncluttered tree may result in energetic savings. In addition, bats are susceptible to aerial predators, such as hawks, falcons, and owls (Barclay et al. 1982; Fenton et al. 1994) as they enter and leave their roosts. The ease with which bats enter and leave their roosts will determine the length of time they are exposed to predation, and thus bats may select tall, uncluttered trees that provide easy access. It is also likely that large, uncluttered trees are easier to find than trees concealed by the canopy, and may stand out as landmarks to bats flying over the canopy surface, assisting in roost relocation (Vonhof and Barclay in press).

Big brown bats and silver-haired bats preferred roosts in trembling aspen trees. The preference of big brown bats for trees with a greater percentage of bark and fewer limbs remaining in part explains their

preference for trembling aspen, which has these characteristics relative to other available tree species. The tree species and decay-stage preferences of cavity-roosting bats are closely tied to the preferences of PCES and to the dynamics of natural-cavity formation (Vonhof and Barclay in press). In the northwestern United States and in British Columbia, in areas with similar forest types to those in the POV, PCES prefer trees with decayed heartwood but relatively hard sapwood, such that there is a hard outer shell surrounding a relatively soft tree core (McClelland et al. 1979; Harestad and Keisker 1989; Lundquist and Mariani 1991). Natural cavities with similar characteristics may form, provided that a path for infection is created through limb detachment, lightning strike, frost cracks, or other trunk wounds, or top-breakage (Newton 1994). Trembling aspen trees over 40 years of age almost always harbour heart rot while they are alive (Winternitz and Cahn 1983; C. Steeger, pers. comm.), and provide excellent conditions for cavity excavation by PCES and natural-cavity formation. Consequently, PCES exhibit strong preferences for trembling aspen in many areas (Erskine and McLaren 1972; Winternitz and Cahn 1983; Harestad and Keisker 1989; C. Steeger, pers. comm.), and trembling aspen trees likely provide the greatest number of suitable cavities for roosting bats. In areas where trembling aspen is less abundant, PCES also exhibit preferences for other tree species, such as western larch (McClelland et al. 1979), western white pine (Lundquist and Mariani 1991), and western hemlock (Zarnowitz and Manuwal 1985), which also harbour heart rot while they are still alive (Cline et al. 1980; see also McClelland et al. 1979; Lundquist and Mariani 1991). However, these tree species occur at low densities in the POV.

Compared to big brown bats, silver-haired bats roosted in Douglas-fir relatively frequently. Although avoidance of Douglas-fir by some PCES has been noted (Crockett and Hadow 1975; McClelland et al. 1979), species such as red-breasted nuthatches strongly prefer to excavate cavities in Douglas-fir killed by *Armillaria* spp. (C. Steeger, pers. comm.), and it was in these cavities that the silver-haired bats roosted. Douglas-fir tends to decay from the outside in, so that decay softens the sapwood before it affects the heartwood (Cline et al. 1980). Therefore, cavities in Douglas-fir tend to break down relatively quickly and may be available to bats for only a short time. However, the high densities of Douglas-fir snags in the POV likely results in at least some suitable cavities being available to bats for roosting. The relative impermanence of cavities in Douglas-fir may explain why both species preferred to roost in more durable cavities in trembling aspen. In other areas of British Columbia, where greater numbers of alternatives are available, no bats have been found roosting in Douglas-fir, even though it is relatively abundant (Vonhof and Barclay in press).

#### MANAGEMENT IMPLICATIONS

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Current forest-harvesting practices and increased hydroelectric developments, with associated increases in the number of cutlines and increased water fluctuations along reservoirs, may significantly reduce suitable habitat for tree-roosting bats. This practice—common to the POV of putting

in relatively large cutblocks separated by small strips of forest—removes large portions of the available roosting habitat, and because older-aged stands are most often targeted in forest-harvesting operations, the remaining forested areas are often deficient of suitable roosting habitat. Similarly, cutlines remove large tracts of forest, and are often developed with little consideration of the kinds of forest that are removed. Older-aged stands contain a greater abundance of large snags in a variety of decay classes (Cline et al. 1980) and are characterized by reduced tree densities, more canopy gaps, and less clutter (Franklin et al. 1981). Thomas (1988) found that bat activity was high in old-aged forest stands in Oregon for the first fifteen minutes after sunset, and suggested that bats use older stands for roosting. However, similar conditions to older-aged stands may be provided in second-growth stands in which large trees were retained, and bats in this study roosted equally often in large trees in older-aged stands or in remnant trees in second-growth stands. If forest stands are intensively managed or are on a relatively short-rotation cycle, the number of large, older-aged trees that are suitable for roosting will decrease.

Although leaving small numbers of trees within cutblocks has been shown to provide habitat for some cavity-nesting birds (e.g., Morrison et al. 1983), I do not believe that this practice can be applied to the management of tree-roosting bats. I did not find any bats roosting in trees left standing in clearcuts, and roost trees tended to be situated within forest stands, rather than in the open. Tree-roosting bats tend to switch roosts frequently, and subsequent roost trees were situated within a relatively small area (Brigham 1991; Lewis 1995; Vonhof 1995a, b). Providing small numbers of trees in an open cutblock will not provide the range or number of alternative trees necessary to meet the needs of bats, and the trees left standing will likely have very different thermal characteristics and provide different degrees of protection from predators than trees within the forest. Only by providing relatively large areas of intact forest will the requirement of bats for small numbers of suitable alternative roost trees within forest stands be met.

Selection harvesting may be a more suitable approach to integrate forestry and bat habitat than clearcutting. Prescriptions that involve selective removal of understorey trees while maintaining veteran and dominant trees (e.g., diameter-limit cut) could reduce the level of clutter in dense, second-growth stands, while preserving the largest and most valuable wildlife trees, and maintaining some degree of canopy cover and associated microclimate. Periodic, low-intensity burning in these selectively harvested stands would help to maintain a more open habitat over time. Other management techniques that accelerate green-tree decomposition and increase wildlife-tree recruitment rates in forested areas (e.g., tree topping with a feller buncher) may enhance habitat for wildlife-tree-dependent species, including bats.

Bats roosting in cavities depend to a greater extent on the dynamics of cavity formation, and the preferences of PCES, for roosting sites. Managing for PCES has been suggested as a means to maintain secondary-cavity-user populations, the idea being that if the requirements of PCES are met, then so will those of secondary cavity users (Brawn and Balda 1983). However, this may not always be the case, and more attention should be focused on determining the rates of cavity turnover and cavity densities (Sedgewick

and Knopf 1992). Considerably larger numbers of cavities may be required in a given area if competition for cavities among tree-dwelling species is strong. Thus, to ensure an adequate supply of cavities for cavity-roosting bats, it will also be necessary to determine the presence and needs of other secondary cavity users in the same area.

Protecting large patches of trembling aspen trees, which bats (this study, Crampton 1995; Kalcounis, pers. comm.) and PCES (e.g., Erskine and McLaren 1972; Winternitz and Cahn 1983; Harestad and Keisker 1989) strongly prefer, should be a management priority. The density of available trembling aspen trees in the POV is relatively low, and thus areas that contain this species should be carefully managed. By protecting stands of trembling aspen to promote natural-cavity formation and meet the requirements of PCES, a reasonable number of available cavities for tree-roosting bats should be maintained. Available Douglas-fir trees occur at high densities in the POV, and the large number of *Armillaria* spp. root-rot centres in the POV should also provide cavities for silver-haired bats.

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*Tree Characteristics*

Diameter at Breast Height (DBH)

Tree Height

Tree Height Relative to Canopy Height

Percentage of Bark Remaining

Number of Limbs

Horizontal Distance to Nearest Neighbouring Tree

Height of Nearest Neighbouring Tree

Horizontal Distance to Nearest Tree of the Same or Greater Height

Height of Nearest Tree of the Same or Greater Height

Horizontal Distance to Nearest Available Tree

*Site Characteristics*

Aspect

Slope

Percentage of Canopy Closure

Canopy Height

Number of Canopy Layers

Horizontal Distance to Nearest Edge

Deciduous Tree Density

Coniferous Tree Density

Available Tree Density